# On the stability of mixed grasslands

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# On the stability of mixed grasslands

R.P.O. Schulte

**Proefschrift**

ter verkrijging van de graad van doctor

op gezag van de rector magnificus

van Wageningen Universiteit,

Prof. Dr. Ir. L. Speelman

in het openbaar te verdedigen

op woensdag 7 maart 2001

des namiddags om half twee in de Aula.

Schulte, R.P.O.

On the stability of mixed grasslands. / R.P.O. Schulte

Ph.D. Thesis, Wageningen University, -With references-, With summary in Dutch.

ISBN: 90-5808-378-0

Subject headings: stability, variability, ecosystem, grassland, white clover, *Trifolium repens*, legumes, mixtures, model, competition, methodology, dry weight rank, organic farming.

# Propositions

1. An increase in the ecosystem dynamics may be the key to achieving stability of grassland production. *This thesis.*

2. Yield fluctuations observed in grassland experiments of short duration (< 5 years), hardly reflect the intrinsic properties or the effects of the management of the ecosystems studied in these experiments, but mostly reflect the influence of the environment during these experiments, instead. *This thesis.*

3. The behaviour of mixed pastures can only be understood by studying plant processes at a hierarchy of spatial scales. *This thesis.*

4. In the natural world, *ceteris non paribus* is the rule.
*Hillel, D. (1993). Science and the crisis of the environment. Geoderma 60, 377-382.*

5. The performance of white clover under sheep grazing can be increased and subsequently maintained, by reducing the sheep residence time per paddock to one day and half a week, respectively.

6. Gastro-intestinal parasite infestations in organic lambs can effectively be reduced by avoiding the use of Suffolk rams.

7. Organic farmers are not excluded from the dilemma between environment and economy, as the use of red clover instead of white clover may increase productivity, yet compromise the nitrogen efficiency at farm level.

8. The Rural Environment Protection Scheme has increased the quantity, yet decreased the quality of Organic Farming in Ireland.

9. Attempts to abandon the compulsive straw-bedding of cattle on organic farms in Ireland illustrate that knowledge and power are sometimes mutually exclusive.

10. Be subtle in your approach, yet daring in its execution.
*Charlie from Fair City.*

11. Chances of one in a million happen nine out of ten times.
*Terry Pratchett, Ian Stewart & Jack Cohen: The Science of Discworld.*

Propositions belonging to the thesis of R.P.O. Schulte, *On the stability of mixed grasslands.*
Wageningen, 7 March, 2001.

**To Polly**

*for everything*

and for everything to come

# Notes

This project was funded by a Walsh Fellowship of Teagasc, the Irish Agriculture and Food Development Authority, and was carried out at the Johnstown Castle Environmental Research Centre, Wexford, Ireland.

Chapters 2 to 7 have been submitted for publication in international journals.

# Abstract

Recent years have seen a renewed interest in the use of white clover (*Trifolium repens*) in grasslands, as a more sustainable alternative to fertiliser nitrogen inputs. However, mixtures of grasses and white clover have frequently been associated with unstable and hence unreliable herbage yields. The maintenance of a stable production from mixed grasslands requires the prototyping of new grassland management strategies.

Temporal yield fluctuations may result from intrinsic ecosystem fluctuations, from environmental fluctuations, or from both. The stability of ecosystems in isolation of their environment is defined as the intrinsic stability. The stability of systems subjected to seasonal environmental fluctuation only is defined as the extrinsic stability, while the stability of systems under a regime of both seasonal and stochastic environmental fluctuations, as measured in field experiments, is defined as the actual stability. The actual stability depends on coincidental weather events and is hence an unreliable reflection of the grassland ecosystem or of the management imposed.

A mathematical framework is presented with which the extrinsic and intrinsic stability levels of grassland ecosystems can be deducted from their yields during a large number of years, and with which the effects of intrinsic system properties and of environmental fluctuations on the stability of their yields can be segregated. Intrinsically stable systems remain stable in the face of seasonal environmental fluctuations, but are destabilised by stochastic environmental events. Intrinsically unstable systems are instead stabilised by environmental seasonality, and may be further destabilised or stabilised by stochastic fluctuations, depending on the timing of individual environmental events.

This framework was applied to the yield data of two long-term experiments. Regular lime applications and a grazing regime increased the extrinsic stability of grassland ecosystems, whereas fertiliser treatments only had small or inconsistent effects. It was consequently hypothesised that the extrinsic stability of ecosystems depends largely on the availability and turnover rate of nutrients.

Vertical spatial interactions between grass species and white clover depend on the vertical distributions of their lamina and total leaf material. A mechanistic model is presented, with which the distributions of perennial ryegrass (*Lolium perenne*) and white clover can be accurately simulated for a wide range of sward types subjected to various management regimes. This model uses simple morphological features of both species as input variables.

The lateral spatial heterogeneity of mixed grasslands was quantified, using data generated by the Dry Weight Rank method for botanical assessment of grasslands. The heterogeneity of the total herbage mass was highest after cutting and topping events, and under lenient grazing, and

lowest under strip-grazing. Opposite responses to the grassland management were found for the heterogeneity of the white clover herbage mass.

The performance of white clover may be compromised by infestations of creeping bentgrass (*Agrostis stolonifera*). A mathematical methodology, based on the Dry Weight Rank method, is presented with which the effects of niche-differentiation and direct competition between white clover and creeping bentgrass can be discriminated. The exclusion of white clover by creeping bentgrass foremost resulted from direct competition. Both species only showed niche-differentiation in response to two extreme management strategies. Whereas the clover performance was enhanced under a permanent cutting regime, creeping bentgrass prevailed under a regime of lenient grazing.

Finally, two types of management strategies were proposed to maintain the production stability of mixed grasslands. Structural management strategies, such as lime applications, the maximisation of the grazed area, and the targeted use of mixtures of grassland species and varieties, aim to increase the extrinsic stability of ecosystems, and can be prototyped. Dynamic management strategies are required to counteract the fluctuations of the abiotic and the biotic environment, and cannot be generalised due to the individuality of each farm ecosystem.

Additional key-words: stability, variability, ecosystem, grassland, white clover, *Trifolium repens*, legumes, mixtures, model, competition, methodology, dry weight rank, organic farming.

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# Preface

In Science, chances of one in a million happen nine out of ten times[1], which can be readily confirmed by a quick browse through the literature. Maybe this explains my luck in getting the opportunity for this research, and especially in having two such colourful teams on both sides. On this side of the Irish Sea, I was given the privilege to work in the country I had always dreamt of, and to fully exploit my passion for farming, firmly with both knees in the grass. At the same time, I was blessed by the ceaseless backup of my supervisors in Wageningen, The Netherlands, who encouraged me to exploit new grounds in the scientific landscape.

This project was funded by a Walsh Fellowship of Teagasc, the Irish Agriculture and Food Development Authority, and carried out at the Johnstown Castle Environmental Research Centre in Wexford, Ireland. I am very grateful to my supervisors Dr. Brian Coulter and Mr. Willie Murphy for their support throughout this project and for keeping all my wild ideas on a straight line. I owe much to Dr. Owen Carton, who was just in time to drag me away from castrating bullocks and to plunge me behind my computer, instead. Thank you for the "chats" when they were most needed. I thoroughly enjoyed working with Dr. Noel Culleton, and especially all our heated discussions and the inspiration he gave me to look further than at clover alone. I firmly believe that not only I, but all organic farmers in Ireland owe you. Also a big Thank You to Mr. Frank Codd, Mr. Rioch Fox, Mr. Nicky Hayes, and Mr. John Murphy for putting up with all my odd requests at the busiest of times. And of course my work would have been half as pleasurable, if not impossible, without the support and friendliness of all the staff in the labs, the castle, and on the farms.

I am equally grateful to the supervising team at the Department of Plant Sciences of the Wageningen University, Wageningen, The Netherlands, for blowing gale force winds into my sails throughout this project. A very special Thank You to my promotor Prof. Dr. Ir. Paul Struik, for his continuous and strengthening backup, and also for his rapid reading of the manuscripts and his unfortunately equally rapid style of writing. I feel privileged to have worked under your supervision. I am as much indebted to my co-promotor Dr. Ir. Egbert Lantinga and to Drs. Jan Neuteboom, for sharing their passion for farming and science, for their inspiration, their sharp discussions and contributions, their journeys to Ireland, their whiskey, and the long, long chats by the stove. I am sure the end of this project does not imply the end of the latter. I also wish to thank Prof. Dr. Ir. Eric

[1] T. Pratchett, I. Stewart & J. Cohen: The Science of Discworld.

Goewie and Ir. Gerard Oomen, who initiated this programme and who put me on the rails in the first place, which turned out to be only a minute step for mankind, but a giant leap for me. The support of all of you meant a lot more to me than supervision alone.

I owe gratitude to many, many more people, whose inspiration and cooperation were indispensable during this project. I wish to thank Dr. Finnain McNaeidhe, the many organic farmers in Ireland, as well as the Irish Organic Farmers and Growers Association for their time and their help. I am delighted to have been introduced to Dr. Tony Brereton, to whom I am much indebted for his time, but foremost for his inspiration. I owe much to Mr. Tony Hegarty, Teagasc Headquarters, for his friendliness, his help and his ability to explain statistics in English. I am very grateful to Dr. Paul Poulton of the Rothamsted Experimental Station, Harpenden, UK, and to Drs. Thies Oomes, Plant Research International, Wageningen, The Netherlands, for their kindness and for the use of the databases of the Park Grass Experiment and the Ossekampen, respectively. I also wish to thank Dr. Adrie Jacobs of the Department of Meteorology and Air Quality of the Wageningen University, Wageningen, The Netherlands, who kindly provided me with the meteorological data required, and who shares my lonely battle against the application programs of a well-known software giant. A very special thanks to Mr. Pieter de Wolf for his assistance and his meticulous work. I will carry fond memories of the late Ir. Klaartje Derks, not only for her excellent work, but especially for the sunshine she brought along.

I owe the Biggest Thank You to my wife Paulette, my family, and all my friends both in Ireland and Holland, for being so patient and for all your support throughout. Be prepared: I'll be back ! Finally a sincere apology to Mr. Koop Wind and Mr. Ton Elzebroek, who sacrificed their agenda and their documents to the Advancement of Science.

# Chapter 1: General introduction

In this thesis, the production stability of mixed grasslands is studied. The need for research on this topic is discussed in this chapter, as well as the approach taken to analyse this production stability. Consequently, the specific objectives of this project and the structure of this thesis are listed.

## 1.1 Background

Recent concerns about the environmental sustainability of the usage of nitrogen fertiliser in North-West European grasslands have increased the interest in the use of legumes, in particular of white clover (*Trifolium repens*), for the nitrogen supply of these grasslands (Parsons *et al.*, 1991a,b; Laws & Newton, 1992; Schwinning & Parsons, 1996a). However, fluctuating and unreliable levels of herbage production have been reported to arise from these mixed grasslands (Curll *et al.*, 1985a,b; Evans *et al.*, 1990; Orr *et al.*, 1990; Laws & Newton, 1992; Schwinning & Parsons, 1996a,b; Fothergill *et al.*, 2000). This unreliability is most eminently illustrated by the notorious "clover crashes", i.e. the sudden extinction of white clover in highly productive mixed swards (Fothergill *et al.*, 1996).

Whereas the management of grass monocultures largely relies on abiotic inputs, the management of mixed pastures encompasses the control of the biotic factors which define the productivity and subsequently the nitrogen fixation of white clover. Therefore, the successful maintenance of a stable herbage production in clover-driven swards requires an understanding of the factors in grassland ecosystems which regulate the performance of white clover.

Numerous studies have focussed on the impact of single aspects of grassland management strategies (e.g. stocking rates, fertiliser inputs, clover varieties) on the production *level* of mixed swards on the short term (< 5 years), which will be reviewed extensively in Chapter 2. In contrast, analyses of the production *stability*, i.e. the reliability of mixed grasslands over a longer period of time, are scarce (but see Thornley *et al.*, 1995; Schwinning & Parsons, 1996a,b). As a result, there is a lack of understanding of the factors regulating production stability, and more importantly for practice, a lack of management strategies which ensure the constancy of herbage production of mixed swards on the longer term (> 5 years). The need for these strategies is particularly prominent in organic farming systems, in which artificial fertiliser nitrogen inputs are disallowed. Nevertheless, also non-organic farming systems using white clover could benefit from the prototyping of these management strategies, as the reliance on nitrogen fertiliser could be reduced by these.

## 1.2 Approach

Originally, the research project undertaken by the author of this thesis merely aimed to prototype grassland management strategies which maximise the production stability of mixed swards, based on evidence from field trials. However, three complications were encountered at an early stage of this project. Most pronouncedly, no existing methodologies were available, that enable the analysis and the quantification of the stability of production of mixed swards. In most studies, the temporal yield patterns of ecosystems are merely classified as stable or unstable, or as showing damped or sustained oscillations (e.g. Noy-Meir, 1975; Parsons *et al.*. 1991b; Thornley *et al.*, 1995; Schwinning & Parsons, 1996a,b; Thornley, 1998). The quantitative comparison of the impact of various grassland management strategies on stability necessitates a comprehensive analysis and quantification of stability.

Secondly, it soon became obvious that grassland stability cannot be understood solely by the analysis of individual factors which were presumed to regulate stability. The production of mixed grasslands depends on biotic nitrogen inputs and hence on the performance of white clover. White clover growth is not only affected directly by the grassland management, but additionally by the environment and by the performance of other species, notably of grasses, which are also influenced by the management imposed. As a result, the responses of the entire grassland ecosystem to management strategies and to the environment need to be understood and taken into account in the study of stability.

Finally, most grassland studies implicitly assume a spatial uniformity of the sward, both vertically and laterally, as the literature commonly reports only the *average* productivity, clover content, *etcetera*, of swards. Although this assumption may arguably apply to grass monocultures, mixed grasslands are generally characterised by spatial heterogeneity, resulting from local urine and manure depositions, non-uniform soil conditions and the growth and colonisation patterns of individual plant species. This means that within a certain field, a variety of herbage masses, and hence a variety of responses to the environment and the management may be observed. As a result, the observed behaviour of ecosystems is largely dependent on its heterogeneity and on the spatial scale at which it is studied (Oldeman, 1990; Collins, 1995). Nonetheless, methodologies allowing for the accurate recording of this spatial heterogeneity, and of the variety of spatial plant responses within fields were not found in the literature.

In summary, it appeared that the behaviour of white clover can only be analysed when the behaviour of the entire ecosystem, as well as the effects of the environment and of temporal and spatial dimensions are accounted for. In this thesis, mixed grasslands are therefore studied as

ecosystems, following a four-dimensional approach, i.e. considering temporal, vertical and the two-dimensional lateral dimensions.

## 1.3 Objectives

This thesis has both scientific and applied objectives. Primarily, it aims to present a comprehensive concept and a quantification of the production stability of grasslands. To date, the few studies in which the stability of grasslands has been the focus of attention (e.g. Parsons *et al.*. 1991b; Thornley *et al.*, 1995; Schwinning & Parsons, 1996a,b; Thornley, 1998) implicitly expanded on the classic concept of Noy-Meir (1975), which assumes the occurrence of static equilibria in grassland ecosystems, in which the system remains stable. However, Noy-Meir's concept presumes a constant environment and a constant management. Moreover, it does not include temporal, nor spatial dimensions. As a result, a discrepancy is identified in this thesis between this concept of stability on the one hand, and experimental evidence on the other.

Therefore, the objective of the current study was to develop a new concept of grassland stability, which does not solely consider grassland ecosystems in isolation, but instead places them in a three-dimensional space and in time, exposed to a variable management in a variable environment. This new concept is intended to bridge the gap between the results of theoretical ecosystem studies and experimental agronomic evidence.

Secondly, this thesis projects to develop a methodology with which stability over time can be measured and quantified over time. This quantification is aimed to allow for more accurate comparisons between the stability properties of different ecosystems, and between the effects of grassland management strategies on the behaviour of ecosystems, than the mere classifications of stability mentioned above.

Considering the impact of the spatial heterogeneity of mixed grasslands ecosystems on their stability levels, additionally methodologies are presented which quantify both the vertical and the lateral heterogeneity of mixed swards, as well as a methodology which allows for the detection and quantification of spatially explicit interactions between plant species.

Finally, using this new concept and these new methodologies, an attempt is made to initiate the identification of grassland management strategies which ensure the production stability of mixed grasslands at a small (i.e. patch) scale, at field scale, and at farm scale.

In conclusion, rather than conclusively prototyping entire grassland management systems, this thesis should instead be considered as a precursor for further and more applied research. It is primarily envisaged to develop a "language" with which the complexity of grassland stability can be comprehended.

## 1.4 Structure

This thesis consists of two discrete parts. In Part I, the temporal production patterns of mixed grassland ecosystems are analysed, and their dependence on intrinsic ecosystem properties, on the grassland management, and on the environmental variability. In Part II, the spatial heterogeneity of mixed swards is explored and quantified, as well as its effects on the stability of production.

First, the classic concept of grassland stability is reviewed in Chapter 2. Effects of intrinsic ecosystem factors and of environmental factors regulating grassland yield patterns over time are explored by means of a simple simulation model and by a review of the existing literature. Consequently, a new concept, as well as new definitions of ecosystem stability are outlined. In Chapter 3, a mathematical framework is presented with which production stability can be quantified. This quantification enables the segregation of the effects of intrinsic ecosystem factors and environmental variability on the yield patterns over time. In Chapter 4, this framework is applied to the data of two long-term grassland experiments, i.e. the Park Grass Experiment (UK) (Anonymous, 1991) and the Ossekampen (The Netherlands) (Elberse *et al.*, 1983), in order to test this framework and the new concept of stability. Additionally, a number of management strategies are identified which increase the stability of mixed grasslands.

In Part II, spatial aspects of grassland stability are explored. Chapter 5 presents a mechanistic model, which enables the quantification and simulation of the vertical heterogeneity of mixed swards. This model can readily be incorporated in existing dynamic grassland simulation models, in order to increase the accuracy of their simulations, and in order to study the impact of the vertical heterogeneity of the herbage mass on the behaviour of mixed swards. In Chapter 6, the lateral heterogeneity of the herbage mass of these swards is quantified, using data generated by the Dry Weight Rank method for botanical assessment of grasslands ('t Mannetje & Haydock, 1963). Subsequently, the impact of a number of grazing management strategies on this heterogeneity is explored. In Chapter 7, a methodology is presented which quantifies and discriminates the effects of two types of spatially explicit interactions between plant species, i.e. direct competition and niche-

differentiation, on the white clover performance. Using this methodology, which is also based on the Dry Weight Rank method, grassland management strategies are identified which maximise the performance of white clover, and minimise pasture infestations by creeping bentgrass (*Agrostis stolonifera*), which is a common weed in Irish grasslands. This methodology could equally be applied to grasslands with other botanical compositions.

The picture is completed in the General discussion, in which the stability concepts of Noy-Meir (1975) and of this thesis are compared and discussed. Consequently, a number of management strategies is proposed, with which the production stability of mixed grasslands can be safeguarded on the short and on the long term. Finally, scientific areas in need of further development are identified, as well as the approaches required for a further study of grassland stability.

# Part I:

# Temporal aspects of grassland stability

# Chapter 2: A conceptual framework for the qualification of production stability in grassland ecosystems

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## Abstract

1) The increased use of white clover in grasslands has led to new management challenges, as mixed pastures have been associated with unstable herbage production. The stability of mixed pastures depends on a complex of intrinsic ecosystem properties, on the spatial and temporal scale at which it is studied, and on the variability of the environment.

2) In this chapter, intrinsic ecosystem properties and processes are explored and illustrated using a simple dynamic simulation model of grass and clover interactions. Competition for light, the delayed availability of nitrogen fixed by white clover, grazing *per se*, preferential grazing for clover, and cutting were identified as destabilising processes. Instead, niche-differentiation, nitrogen dependence of grass and clover, and plant mechanisms to "escape" from grazing, were identified as stabilising processes. The intrinsic stability of mixed swards depended on the balance of, and the interactions between these processes.

3) It is explained how spatial heterogeneity can stabilise ecosystems which oscillate at patch scale. Heterogeneity can be maximised by increasing the incidence of small-scale disturbances and by minimising large-scale disturbances.

4) Including the temperature as an environmental variable into the model, unstable ecosystems were stabilised by seasonal temperature fluctuations, and were either further destabilised, or stabilised by stochastic temperature fluctuations. Stable ecosystems were always destabilised by these stochastic fluctuations.

5) Finally, three concepts of stability are presented. The actual stability is defined as the stability of grasslands as measured in the field, i.e. subjected to both seasonal and stochastic environmental fluctuations. The extrinsic stability presumes the presence of seasonal, yet the absence of stochastic environmental fluctuations. The intrinsic stability represents the stability of yields in a hypothetical constant environment.

6) It is explained how these concepts of stability can bridge the gap between experimental and theoretical studies. It is demonstrated that long-term experiments are required for the experimental analysis of grassland stability, and it is argued that the development of spatially

and environmentally explicit simulation models is a prerequisite for the prototyping of management systems for mixed grasslands.

## 2.1 Introduction

Recent years have shown a renewed interest in the use of legumes in pastures, in particular of white clover (*Trifolium repens*), as a more sustainable alternative to fertiliser nitrogen (Parsons *et al.*, 1991a,b; Laws & Newton, 1992; Schwinning & Parsons, 1996a). Whereas the herbage production of grass monocultures under a fertiliser regime can be controlled to some extent by fertiliser inputs and grassland management strategies, the maintenance of stable and productive mixed swards has been a challenge to date. Fluctuating performances of mixed pastures have frequently been reported (Curll *et al.*, 1985a,b; Evans *et al.*, 1990; Orr *et al.*, 1990; Laws & Newton, 1992; Schwinning & Parsons, 1996a,b; Fothergill *et al.*, 2000). The reliability of herbage production is a prerequisite for the managerial decision making by individual farmers. Hence the production stability of mixed pastures over several years is as important to the livestock industry as is the level of production itself (Curll, 1982; Fothergill *et al.*, 2000).

Grassland ecosystems can be studied either in agronomic experiments, or by using ecological models. To date most experimental agronomic studies have focussed mainly on the level of production. Unfortunately, the duration of these experiments is commonly limited to a maximum of four or five years, which is too short to allow an analysis of the stability of production. One of the exceptions to this rule is the Park Grass Experiment (Collins, 1995), in which yields of a large number of experimental plots have been recorded for well over a century (e.g. Silvertown, 1980; Silvertown & Dodd, 1994; Dodd *et al.*, 1995).

In these agronomic studies, grassland stability is frequently defined as the inverse of the variation of yields among years. However, this variation depends both on intrinsic ecosystem properties, and on the variability of the environment during the observation period. For example, a grassland system observed during a period of transient drought, heat, rain and frost, is bound to show a high variability of yields. Although the impacts of intrinsic properties and environment on *yield* can sometimes be separated (e.g. Barthram *et al.*, 1992; Silvertown & Dodd, 1994), the discrimination of their respective impacts on the *stability* is highly complex. Due to the dependence of the observed stability level on environmental fluctuations, this level is restricted to a limited environment during a limited period, disabling a fair comparison of the stability of ecosystems which are separated in either time or space.

Stability has received more attention in theoretical ecological studies, in which the behaviour of ecosystems is analysed using mechanistic models. In a now classical publication, Noy-Meir (1975) transformed the predator-prey model by Rosenzweig & MacArthur (1963) into an ecological model, applicable to agricultural grassland ecosystems. Recently, increasing computer power has enabled the development of increasingly complex dynamic simulation models, in which pasture processes are simulated over time (e.g. Grenfell 1988; Thornley & Verberne, 1989; Parsons *et al.*, 1991b; Parsons *et al.*, 1994; Schwinning & Parsons, 1996a,b; Thornley *et al.*, 1995; Thornley, 1998; Brereton & McGilloway, 1999). These models can simulate numerous possible ecosystems in various hypothetical environments, thus allowing a mechanistic analysis of the processes regulating ecosystem stability. Nevertheless, this approach, too, has serious limitations.

Firstly, the predictions on stability largely depend on the structure of the model itself. For instance, Schwinning & Parsons (1996a) reported that the predictions on stability changed fundamentally when they simplified their grass-clover model from eight to four state variables. In their following paper (Schwinning & Parsons, 1996b) an even more drastic change was observed when spatial (lateral) interactions were included in the model. In an earlier model, Parsons *et al.* (1991b) simulated competition between grass and clover under various defoliation regimes. This model did not include nitrogen fixation by clover, and therefore its long term predictions were mostly biassed towards a high ryegrass content and clover extinction. In these cases the boundaries and the structures of the models had a definite impact on their predictions.

Secondly, simulation models commonly analyse the intrinsic ecosystem properties in isolation of the environment, presuming either constant (e.g. Noy-Meir, 1975; Grenfell, 1988; Parsons *et al.*, 1991b) or sinusoidally fluctuating (e.g. Thornley 1998) environmental variables. However, the impact of stochastic environmental events is decisive for both the level and the stability of production. Nonhebel (1994) studied the effect of using average weather data (ten-daily, monthly, or seasonally) instead of daily weather data in a wheat growth simulation model, and found that the use of the former led to yield overestimates of less than 15% in wet conditions, and to underestimates up to 50% in dry conditions. These differences arose from non-linear responses of the system to environmental variables such as temperature and precipitation. However, the growth period of wheat did not exceed 6 months in any case, which limited the accumulation of under and overestimations. Larger discrepancies caused by using daily instead of average or seasonal weather data may be expected in grassland simulations, which may cover growth periods up to 10, 100, or even 1000 years (e.g. Thornley, 1998).

Finally, "stable" grassland systems are often associated with systems in equilibrium, i.e. systems in which all state variables remain constant (e.g. Noy-Meir, 1975), or return to their initial values each year, in case environmental seasonality is incorporated into the model (e.g. Thornley,

1998). System stability is then implicitly defined as the capacity to remain in equilibrium in the face of environmental perturbations. In fact, stability is here confused with the combined resistance (reluctance to change) and resilience (recovery capacity) of the system. In contrast, real ecosystems are continuously exposed to stochastic environmental events, and are therefore constantly "pushed out of" their equilibria. Moreover, the positions of the equilibria are largely defined by environmental variables, which may change too rapidly for the ecosystem to respond and to return to its equilibrium. A rather spectacular example of the latter phenomenon is given by Thornley (1998), who examined a modelled grazing system of Noy-Meir (1975). Noy-Meir's original system was discontinuously stable, showing two equilibria, one at a low and one at a high Leaf Area Index. When this system was reproduced at a higher temperature (20°C instead of 10°C), this bifurcation disappeared, resulting in an ecosystem with only one equilibrium. Such a change of temperature can readily be achieved *within one day* in temperate climates, and therefore the existence of either of the equilibria is only of academic significance.

Summarising, there are two schools of thought in the study of grassland ecosystem stability. The first one is based on experimental research, where the stability of the total yield between years is the primary focus. Unfortunately, the experimental data are limited and dependent on both internal system properties and environmental factors. Their influences are hard to separate, and contain a large amount of "noise". The second school of thought is based on theoretical ecological studies. These can analyse the underlying processes of the stability or instability of grassland ecosystems in isolation of the environment. Nevertheless, the direct applicability of their results into farm practice is questionable, considering the large impact of stochastic environmental fluctuations on the stability of real ecosystems (Chapters 3 and 4). Both approaches complement rather than exclude each other.

In this chapter a conceptual framework for the analysis of grassland stability is presented, which incorporates both the intrinsic properties of grassland ecosystems in isolation, and their responses to the variable environment. This framework is based on a review of the experimental and modelling studies available in the literature. The objective of this study is to derive a universally applicable definition and quantification of grassland stability. The emphasise in this chapter will be on the interaction between white clover (*Trifolium repens*) and perennial ryegrass (*Lolium perenne*), which will generally be referred to as "clover" and "grass". However, extrapolation of the main interactions to other legume and grass species with similar properties is easily envisaged.

First the intrinsic properties and interactions of a grass-clover sward will be summarised. Secondly, the effect of the spatial scale studied on the system stability will be explored, and finally the impact of the environment will be taken into account, leading to a qualification of grassland

stability. The resulting concept of stability will be quantified in the following chapter (Chapter 3), and tested against long-term experimental data (Chapter 4).

## 2.2 Intrinsic ecosystem properties and processes regulating stability

### *2.2.1 Materials and methods*

First a concept is presented of the impact of the intrinsic properties and processes of the ecosystem which regulate stability. This concept is based on the insight into the behaviour of mixed pastures, produced by ecological models. Wherever these findings have been confirmed by empirical data, these will be referenced. To clarify the various stabilising and destabilising processes, these will be exemplified by the step-by-step construction of a simple simulation model, from a monoculture of perennial ryegrass growing under a cutting regime and under constant environmental conditions, to a grazed mixture of grass and clover in a variable environment. *Pro temp.* the herbage mass is assumed to be distributed homogeneously across the field, both vertically and laterally. This model is in fact an alteration and simplification of the model presented by Schwinning & Parsons (1996a). Its mere purpose is to graphically illustrate the stabilising and destabilising ecosystem processes that will be dealt with. To avoid the illusion that it would have any quantitative accuracy, its output is, *sensu* Noy-Meir (1975), only presented relatively, i.e. on a scale from 0 to 1, to the maximum instantaneous herbage mass of a perennial ryegrass monoculture under optimal conditions (for reference purposes only: 1 unit corresponds to *c.* 7000 - 10,000 kg DM $ha^{-1}$). Nevertheless, the model has been constructed in such a way that its predictions agree qualitatively with the results of the far more sophisticated and preferable simulation models which have been produced to date.

### *2.2.2 Growth and senescence*

The starting point is formed by an ecosystem consisting of a grass monoculture only, under an unlimited nutrient supply. This system is here defined by just one state variable, i.e. the total mass of live herbage per unit area. Thornley (1998) needed 44 state-variables to describe this grass monoculture with reasonable accuracy, which underlines the simplicity of the model presented here. The two processes regulating the productivity and stability of this monoculture, which are highlighted here are growth and senescence. Growth is modelled with a well-known saturation function, *sensu* Thornley *et al.* (1995), and based on empirical evidence by Bircham & Hodgson (1983):

$$p_i = p_{max\,i} \cdot \frac{H_i}{H_i + k_{p\,i}} \qquad \text{Eq. 2.1}$$

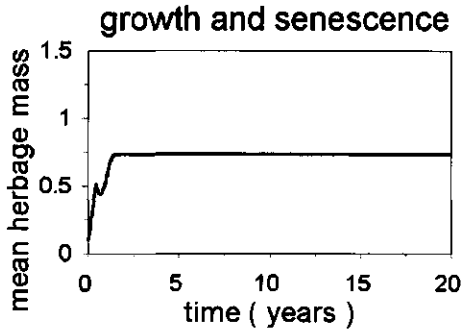


Figure 2.1: Progressive annual mean herbage mass of grass during 20 years, as a result of growth and senescence only.

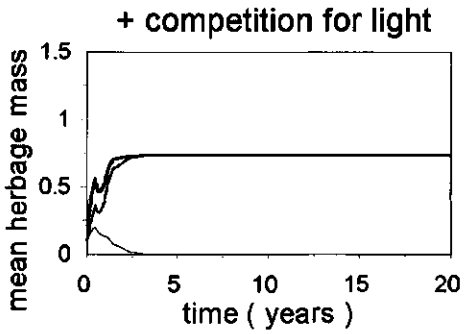


Figure 2.2: The effects of competition for light on the progressive annual mean herbage masses of grass and clover during 20 years. Thin line: clover; single line: grass; bold line: total herbage mass.

in which $p_i$ is the growth rate, $p_{max\,i}$ the maximum growth rate, $H_i$ the total amount of herbage, and $k_{p\,i}$ is a parameter indicating the amount of herbage at which the growth rate is half of its maximum rate. The suffix $i$ takes the value of 1 to indicate grass, and will take the value 2 to indicate clover. In this function the *relative* growth rate ( $p_{max\,i} / H_i$ ) is maximal at low herbage, and progressively reduced by intra-specific competition, as the herbage accumulates. Simplifying Schwinning & Parsons' model (1996a), senescence is assumed to be linearly related to the total amount of herbage as:

$$s_i = d_i \cdot H_i \qquad \text{Eq. 2.2}$$

in which $s_i$ is the senescence rate, and $d_i$ the relative senescence rate.

The effects of growth and senescence were dynamically simulated over time by numerical integration (Euler's method) of equations 2.1 and 2.2, with an integration step of 0.02 years. The initial herbage mass of grass was set at 0.1 units, and each year the herbage mass was reduced by a fraction $c_i = 0.9$ to simulate the cutting of the sward. Figure 2.1 illustrates the pattern of the herbage mass over twenty years. This figure shows the progressive annual mean herbage mass, rather than the instantaneous herbage mass, as the yearly cutting of the sward led to a high variability *within* years of the latter. The irregularity during the first year reflects the first cutting event. Note that (virtual) parameter values have been chosen, which in absence of cutting lead to a maximum amount of herbage of 1 unit in more or less half a year (see appendix).

The growth function is a positive feedback function, as the growth is accelerated as the amount of herbage increases. Contrastingly, senescence is a negative feedback process, decreasing

the amount of herbage and thereby reducing its own rate. Predictably, growth in absence of senescence would lead to forever growing and therefore unstable systems. The result of growth and senescence stabilises the grass system into an equilibrium, at which growth equals senescence.

*2.2.3 Competition for light*

If clover is introduced into this grass monoculture, and if all soil factors (nutrient and water status) are assumed to remain unlimited during growth, then these two grassland species will primarily compete for light. Simplifying Schwinning & Parsons' (1996a) approach, the growth of either species can be described by:

$$p_i = p_{maxi} \cdot \frac{H_i}{H_1 + H_2 + k_{p\,i}} \qquad \text{Eq. 2.3}$$

where the suffix $i$ takes the value of either 1 (grass) or 2 (clover). Adding $H_1$ and $H_2$ proportionally in the denominator, in fact implies that the intra-specific and the inter-specific competition have identical effects on the growth of either species. This unlikely situation can only arise when both species use an identical set of resources, i.e. show no niche-differentiation. Figure 2.2, produced by numerical integration of equations 2.2 and 2.3, shows that under an unlimited supply of other plant resources, the competition for light *per se* (i.e. in absence of other processes) leads to a rapid extinction of the least competitive species, i.e. clover. The initial values of both $H_1$ and $H_2$ were set at 0.1 units, and each year the herbage mass of both species was reduced by fractions $c_1 = c_2 = 0.9$.

Woledge & Dennis (1982) found identical instantaneous $CO_2$ assimilation rates for grass and clover leaves. However, Schwinning & Parsons (1996a) suggested that even when mineral nitrogen is not limiting growth, clover will continue to invest metabolic energy into the nitrogen fixing bacteria, thereby compromising its energy investment in growth. Curll (1982) stated that under lenient grazing clover is unable to raise its leaf canopy to the same height as the grass canopy, resulting in a lower light incidence for clover. Therefore here Schwinning & Parsons (1996a) have been followed, who attributed grass with a competitive advantage for light.

The destabilising effect of light competition is confirmed by experimental data from the Park Grass Experiment (Silvertown & Dodd, 1994). These show that at plots receiving nitrogen, grasses competed successfully with legumes for light. The same observation was made by Nassiri (1998), who studied the regrowth of grass and clover under yearly nitrogen applications of 150 kg N $ha^{-1}$. He showed that asymmetric competition for light between perennial ryegrass and clover was small at the early regrowth stages after a cutting event, when individual leaves of both species may be assumed to be light saturated. However, under a nitrogen regime, clover performance was

progressively compromised during the regrowth period. The destabilising effect was also observed by Parsons *et al.* (1991b), who modelled grass-clover competition for light under continuous grazing, but in the absence of the biological nitrogen fixation by clover, and in absence of competition for nutrients. They consequently stated that mixtures (under these conditions) are intrinsically unstable and tend to lead to stable monocultures.

*2.2.4 Niche-differentiation*

Niche-differentiation comprises the use of (partially) different resources by individual grassland species. The resource usages of two species can be separated either in time, e.g. mixtures of early and late species or varieties (e.g. Culleton *et al.*, 1986) or in space, e.g. mixtures of species with different rooting patterns (R.P. Collins, pers. comm.). But the most important niche-differentiation in grass-clover swards is beyond doubt the separated nitrogen sources of both species, resulting from the fixation of atmospheric nitrogen by clover. However, if clover is supplied with mineral soil nitrogen, e.g. after a fertiliser application, its soil nitrogen uptake will reduce the nitrogen fixation, and eventually exceed it (Schwinning & Parsons, 1996a). Hence the extent of the niche-differentiation is variable, and depends on the management regime.

Niche differentiation for nitrogen was modelled mechanistically by Schwinning & Parsons (1996a), who to this purpose included an organic soil nitrogen and a mineralised soil nitrogen pool into their model. Nitrogen uptake by both species, and nitrogen fixation by clover depended dynamically on the size of these pools. However, the dependence of grass on clover for its nitrogen supply, and the soil processes involved in the nitrogen mineralisation also depended on the dynamics of these nitrogen pools. Therefore their approach does not allow a formal discrimination of the effects of niche-differentiation, dependence, and delayed dependence, which are dealt with below.

In fact niche-differentiation implies that the mutual interference between individuals of one species exceeds the interference between individuals of different species, i.e. the intra-specific competition exceeds the inter-specific competition. Therefore, *sensu* Spitters (1983), a parameter for niche-*overlap* is included in the model here, $n_i$, ranging between 0 and 1, which scales the inter-specific competition relative to the intra-specific competition:

$$p_1 = p_{max1} \cdot \frac{H_1}{H_1 + n_1 \cdot H_2 + k_{p1}} \qquad \text{Eq. 2.4a}$$

$$p_2 = p_{max2} \cdot \frac{H_2}{n_2 \cdot H_1 + H_2 + k_{p2}} \qquad \text{Eq. 2.4b}$$

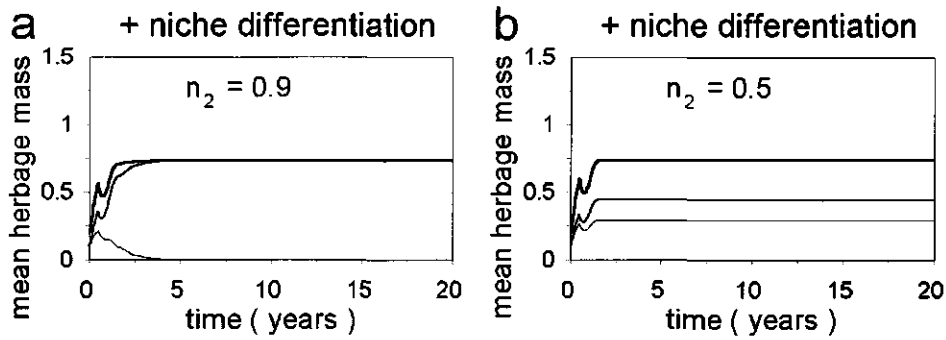


Figure 2.3: The effects of niche-overlap on the progressive annual mean herbage masses of grass and clover. a: $n_2$ = 0.9 (default value); b: $n_2$ = 0.5. In both graphs, $n_1$ = 1. Legend as in Figure 2.2.

For grass-clover it is assumed that $n_1 = 1$, which means that all resources of grass (e.g. mineral N) are also used by clover. However, $n_2 < 1$, as only part of the resources used by clover is also used by grass.

Figure 2.3 shows that niche-differentiation can lead to stable mixtures, in case its stabilising effect compensates for the destabilising effect caused by competition for light, i.e. when the niche-overlap $n_2$ is below a critical value. Note that niche-differentiation may only lead to an increase of the total yield when certain criteria are met, such as a similar production level of both species in monoculture (see Van den Bergh, 1968).

Empirical evidence for the stabilising effects of niche-differentiation was again found in the Park Grass Experiment (Silvertown, 1980). In spite of the fluctuating performances of individual leguminous species, the total fraction of the herbage consisting of legumes remained remarkably stable through time in each plot, indicating a niche for the nitrogen fixating legumes. The size of this niche depended on the fertiliser regime. However, it should be kept in mind that this stability of the botanical composition is not necessarily an indicator of production stability (see section 2.5).

*2.2.5 Dependence*

In absence of fertiliser nitrogen or other external nitrogen inputs, the grass in grass-clover mixtures will largely depend on the fixation by clover for its nitrogen supply. This is referred to as the dependence of grass on clover. It is assumed that the amount of nitrogen fixed by clover is linearly related to its total herbage yield. In fact the relation between clover growth, defoliation, and nitrogen fixation is complex, and extensively explored by Ryle *et al.* (1989). They concluded however, that the rate of nitrogen fixation is regulated to meet the plant's requirement for nitrogen; hence the simplified assumption here, of a linear relationship between the nitrogen fixation rate and

the clover herbage mass. The growth response of ryegrass to available nitrogen is still the subject of debate (Thornley, 1998). Thornley & Verberne (1989) assume a linear response of the maximum photosynthetic rate to the tissue nitrogen content. In a later publication, Thornley (1998) adds a ceiling level to this function. Lantinga *et al.* (1996; their Figure 3) showed that this response depends additionally on the nitrogen application rates. Sheldrick *et al.* (1990) present a complex function with a single maximum, relating total ryegrass yield to the fertiliser nitrogen rate. Here the approach of Schwinning & Parsons (1996a) is modified. They related grass growth to the mineral nitrogen level using a simple saturation function. Considering the assumed linear relationship between clover production and nitrogen fixation, here the mineral nitrogen level is replaced by the total amount of clover herbage. *Pro tem.* this simplification purposely ignores all soil processes involved in the decomposition of nitrogen in senescent tissue into available soil nitrogen, which will be dealt with below. The grass growth rate is now modified to:

$$p_1 = p_{max1} \cdot \frac{H_1}{H_1 + n_1 \cdot H_2 + k_{p1}} \cdot \frac{H_2}{H_2 + k_{dep}} \qquad \text{Eq. 2.5}$$

in which $k_{dep}$ is a parameter indicating the amount of clover (and therefore $N_2$-fixation) needed by grass to achieve its half-maximal growth rate. The default value of $k_{dep}$ is set at 0.02, which corresponds with field data from Wind *et al.* (1993). They monitored yields and the botanical composition of grazed plots where nitrogen applications had ceased, but P and K applications continued. Annual dry matter production dropped from around 9 tonnes $ha^{-1}$ $yr^{-1}$ under nitrogen applications to around 4.5 tonnes $ha^{-1}$ $yr^{-1}$ within three years, while the annual white clover production stabilised at around 0.225 tonnes $ha^{-1}$ $yr^{-1}$. Therefore the ratio between the white clover yield leading to half maximum herbage yield (as opposed to half maximum growth), and the maximum herbage yield equalled 0.025.

Figure 2.4a illustrates the stabilising effect of this dependence *per se* (ignoring the time delay between nitrogen fixation and nitrogen availability) on the stability of the mixture. As the growth rate of grass is progressively inhibited by lack of nitrogen, when the clover content decreases, this dependence now supplies clover a permanent place in the pasture. Note that this dependence and the resulting stability presume the absence of fertiliser nitrogen. This was confirmed by Schwinning & Parsons (1996a), whose model showed that at high fertiliser applications combined with low nitrogen losses, the stabilising effect of dependence is not strong enough to counteract the destabilising effect of competition for light, eventually leading to a grass monoculture. In cases where the dependence of ryegrass on clover is unusually high ($k_{dep}$ = 0.1; Figure 2.4b), the system may be destabilised into a clover monoculture. This was also predicted by Schwinning & Parsons'

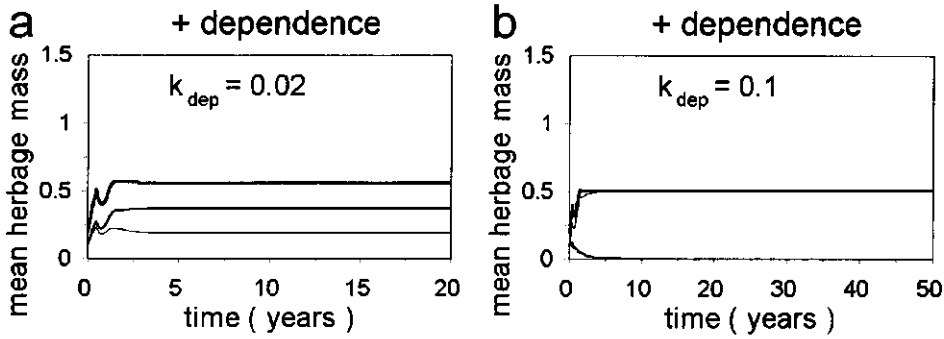


Figure 2.4: The effects of the dependence of grass on clover for its nitrogen supply on the progressive annual mean herbage masses of grass and clover. a: $k_{dep}$ = 0.02 (default value); b: $k_{dep}$ = 0.1 (strong dependence: a clover monoculture remains). Legend as in Figure 2.2.

(1996a) model in absence of fertiliser inputs combined with a high relative leaching rate of mineral nitrogen.

The stabilising effect of dependence is indirectly confirmed by the data from the Park Grass Experiment: Silvertown & Dodd (1994) reported that the variability of yields, caused by the competition for light, was more pronounced on plots receiving fertiliser N. More conclusive evidence was given by Curll *et al.* (1985a). They found that in swards continuously grazed with sheep, the clover content declined to under 10% within one year after reseeding, when nitrogen fertiliser was applied at a rate of 200 kg $ha^{-1}$ $yr^{-1}$, whereas clover was maintained at higher levels between 15% and 50% on unfertilised plots. Barthram *et al.* (1992) found that nitrogen applications reduced branching of clover, leading to lower densities of growing points in mixed swards grazed by sheep. Similar conclusions were drawn by Nassiri (1998), who studied grass-clover competition under a cutting regime, on both fertilised (150 kg N $ha^{-1}$ $yr^{-1}$) and unfertilised plots. Both in spring and summer, the clover which did not receive nitrogen outperformed the clover on the fertilised plots.

### *2.2.6 Delayed responses*

Delayed responses are an important feature in a wide range of ecosystems. They are well-documented and most pronounced in systems where animal species with discrete, non-overlapping generations, e.g. many insect species, play a major role (May, 1976). However, delayed responses have also been reported in grassland studies. Schwinning & Parsons (1996a) mention seed dormancy and maturity effects as possible causes of delayed responses, but emphasise the role of nutrient pools with a slow turnover-rate. In the absence of grazing, nitrogen fixed by clover will only become available when the clover material ages and decomposes. In addition, in their model the slow mineralisation rate of the organic nitrogen pool in the soil profoundly delayed the response of ryegrass to the nitrogen fixation by clover. Delayed responses are destabilising and in most cases

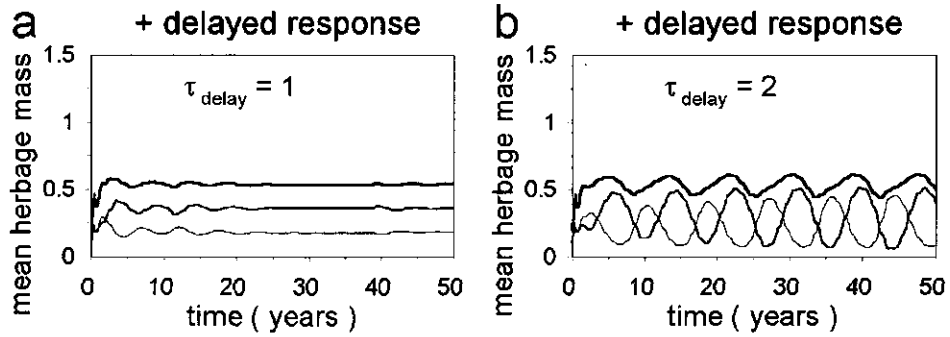


Figure 2.5: The effects of the delayed response of grass to the nitrogen fixation by clover on the progressive annual mean herbage masses of grass and clover. a: $\tau_{delay} = 1$; b: $\tau_{delay} = 2$ (default). Legend as in Figure 2.2. Note the increased time scale on the X-axis, up to 50 years.

lead to damped or sustained oscillatory system behaviour. Schwinning & Parsons (1996a) found sustained fluctuations of grass and clover yields with a periodicity of 4 to 7 years, this periodicity increasing with slower mineralisation rates. Even in absence of legumes, Thornley's model of a grass monoculture produced biennial oscillations which were related to the interaction between plant and soil water status (Thornley, 1998). In "real" ecosystems (as opposed to "model" systems) most of these fluctuations will be either compensated by neighbouring patches fluctuating "out of phase" (see section 2.3 of this chapter), or "hidden" behind the noise of environmental variability (see section 2.4 of this chapter). However, some evidence of a delayed response is again available from the Park Grass Experiment. Silvertown (1980) detected no regular or irregular cycles in the composition of botanical components. Nevertheless, in a more recent publication (Silvertown & Dodd, 1994) a significant and positive correlation was found between the total herbage mass on the one hand, and the fraction of the herbage mass made up by grass species in the following year, on the other. Dodd *et al.* (1995) reported on the occurrence of individual increases and declines of grassland species, as well as periodic oscillations of the presence of species in the same experiment. They related these, however, to the reproductive strategies of the species involved, rather than to the existence of nutrient pools with a slow turn-over rate. Fothergill *et al.* (2000) reported on 3 to 4 year cycles of clover content under continuous grazing. Finally, in a grazing experiment by Curll *et al.* (1985b), stocking rates and nitrogen application had significant effects on the production levels and botanical composition the following year, when all plots were treated identically, indicating delayed responses, or a "system memory".

The current illustrative model focusses merely on the delayed response of ryegrass to the nitrogen fixation by clover. To enable exploration of the effects of delay *per se*, this is implemented

crudely, *sensu* Thornley *et al.* (1995): the production of ryegrass is now directly related to the amount of clover $\tau_{delay}$ years earlier (compare equations 2.5 and 2.6):

$$P_1 = P_{max1} \cdot \frac{H_1}{H_1 + n_1 \cdot H_2 + k_{p1}} \cdot \frac{H_2(t-\tau_{delay})}{H_2(t-\tau_{delay}) + k_{dep}} \qquad \text{Eq. 2.6}$$

in which $t$ represents the time in years, and $\tau_{delay}$ the formally imposed delay period. Figure 2.5 illustrates that this delayed dependence causes the simulated system to oscillate, with oscillations being damped when the delay is relatively short, i.e. 1 year (Figure 2.5a). However, if the delay is doubled to its default value of 2 years, this results in sustained oscillations of both the yield and the botanical composition of the system (Figure 2.5b). Note that the 7.5-year periodicity of the fluctuations in Figure 2.5b exceeds the imposed delay of 2 years, as this periodicity is dependent on both the delay and the actual growth and senescence rates.

*2.2.7 Grazing*

Grazing is arguably the most complex factor in the maintenance of grassland stability, as it involves selective removal of plant tissue, accelerated recycling of nutrients, and dynamic interactions between plants and animals. The effect of grazing *per se*, i.e. the unselective removal of leaf material, has mostly been studied by the use of simulation models. In "real" pastures, grassland plant species may almost by definition have "escape mechanisms" (see below), while grazing animals are bound to show preference for particular species. This disables the empirical study of the grazing *per se*.

The herbage intake rate is a function of sward properties such as the vertical and horizontal dispersion of plant material, as well as of animal properties such as bite area, bite depth, handling time and maximum grazing time (e.g. Parsons *et al.* 1994; Brereton & McGilloway, 1999). In general, the animal intake rate increases with larger amounts of available herbage, to a maximum intake level, which is limited by animal numbers, handling time, and maximum grazing time (Parsons *et al.*, 1994). Here the grazing function of Schwinning & Parsons (1996a) is modified into equations which give the intake rates of grass $g_1$ and of clover $g_2$ , in the absence of escape mechanisms and preference, and which replace the annual cutting of the sward:

$$g_1 = g_{max} \cdot \frac{H_1}{H_1 + k_g} \cdot \left(1 - 0.5 \frac{H_2}{H_2 + k_g}\right) \qquad \text{Eq. 2.7a}$$

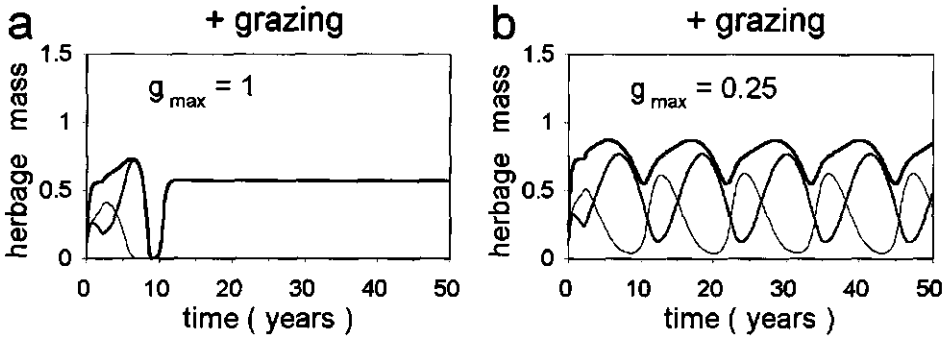


*Figure 2.6: The effects of grazing per se on the herbage masses of grass and clover. a: $g_{max} = 1$ (default); a clover monoculture remains after grass collapses. b: $g_{max} = 0.25$. Legend as in Figure 2.2.*

$$g_2 = g_{max} \cdot \frac{H_2}{H_2 + k_g} \cdot \left(1 - 0.5 \frac{H_1}{H_1 + k_g}\right) \qquad \text{Eq. 2.7b}$$

in which $g_{max}$ is the maximum intake rate of all animals, which is dependent on both the physically maximum intake rate per animal and the number of animals $ha^{-1}$. $k_g$ is the total herbage mass at which the total intake rate is half maximal. The fraction 0.5 in both equations indicates the absence of animal preference for either species.

Figure 2.6 shows the destabilising effect of grazing in the absence of preference and escape mechanisms on the herbage masses of grass and clover. In this case, even at a maximum intake rate ($g_{max}$) as low as 1 (default), corresponding to the maximum intake rate of approximately 1.4 livestock units per hectare, grazing *per se* leads to the extinction of the dependent species, i.e. the ryegrass (Figure 2.6a, in which clover recovers after ryegrass collapses). Only at extremely low stocking rates ($g_{max} < 0.3$) can the growth of ryegrass compensate for the tissue removal (Figure 2.6b).

Using a much more sophisticated model, which did not include niche-differentiation or dependence, though, Parsons *et al.* (1991b) came to similar conclusions. In their model grazing *per se* led to monocultures of clover at all stocking rates. However, in their case this was the result of the higher specific leaf area which had been applied to clover, rather than by the dependence of grass on clover, as is the case in the current model. Noy-Meir (1975) studied the effect of grazing intensity on monocultures, and although his model did not include a temporal dimension, he found that in the absence of escape mechanisms (see below), higher stocking rates increased the probability of a "system collapse" as a result from overgrazing.

In "real" pastures grazing *per se* will usually be accompanied by plant escape mechanisms

and animal preference. Therefore no experimental data were found in the available literature to confirm its destabilising effect as predicted by the model.

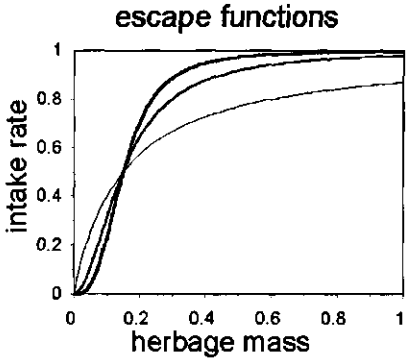


Figure 2.7: The response of the intake rate to the total herbage mass under 3 levels of escape: thin line: $q_{esc} = 1$ (no escape); single line: $q_{esc} = 2$ (default), bold line: $q_{esc} = 3$.

*2.2.8 Escape mechanisms from grazing*

As explained above, the effects of grazing *per se* are only of academic interest, as most grassland plants show mechanisms to escape from being grazed to extinction. These mechanisms involve substrate reserves in roots, stolons, or bulbs, or a prostrate morphology. These keep at least part of the tissue or substrate material out of reach from the grazing animal (Noy-Meir, 1975). At very low herbage amounts, the grazing intensity is then reduced asymmetrically to the amount of herbage. Figure 2.7 (after Noy-Meir, 1975) shows that stronger escape mechanisms lead to increasingly sigmoid grazing functions, with virtually no grazing at very low herbage densities. These sigmoid functions can be produced by adding an escape parameter $q_{esc}$ to equation 2.7, resulting in (modifying Schwinning & Parsons, 1996a; but see also Parsons *et al.*, 1991b):

$$g_1 = g_{max} \cdot \frac{H_1^{q_{esc1}}}{H_1^{q_{esc1}} + k_g^{q_{esc1}}} \cdot \left(1 - 0.5 \frac{H_2^{q_{esc2}}}{H_2^{q_{esc2}} + k_g^{q_{esc2}}}\right) \qquad \text{Eq. 2.8a}$$

$$g_2 = g_{max} \cdot \frac{H_2^{q_{esc2}}}{H_2^{q_{esc2}} + k_g^{q_{esc2}}} \cdot \left(1 - 0.5 \frac{H_1^{q_{esc1}}}{H_1^{q_{esc1}} + k_g^{q_{esc1}}}\right) \qquad \text{Eq. 2.8b}$$

Figure 2.8 shows the stabilising effect of the plant escape mechanism on the grassland system when for both species $q_{esc}$ is set at its default value of 2. (Schwinning & Parsons, 1996a, but see also Parsons *et al.* 1991b). It also shows an important interaction between the escape mechanism and the grazing intensity, as expressed in $g_{max}$ : an increase in grazing intensity does not simply decrease system stability anymore. Instead, both an increase (Figure 2.8b) and a decrease (Figure 2.8c) of the maximum intake tend to stabilise the system. This is further illustrated by Figure 2.9, where the average variability of the system as well as the average actual intake rate, are shown for a range of maximum grazing intensities. Ecosystem variability was quantified as the coefficient of variation of the average yearly herbage mass over a ten-year period (Chapter 3). Both the

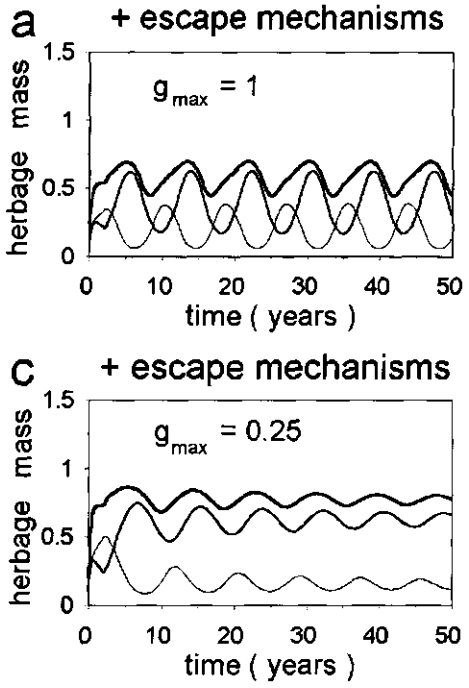


Figure 2.8: The effects of escape mechanisms and maximum intake on the stability of the system. a: $g_{max}$ = 1 (default); b: $g_{max}$ = 2; c: $g_{max}$ = 0.25. $q_{esc}$ = 2 for all cases. Legend as in figure 2.2.

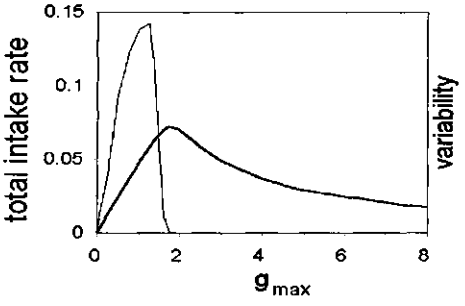


Figure 2.9: The effect of the maximum intake rate on the actual total intake rate (single line) and the system variability (thin line) in the presence of plant escape mechanisms ($q_{esc}$ = 2).

variability and the animal intake show a function with a single maximum. This agrees qualitatively with results by Noy-Meir (1975; his Figure 10), who found low total animal intake rates at both low and high stocking densities, when escape mechanisms were included. At intermediate stocking levels, his model produced a discontinuously stable system which is in equilibrium at either a high or a low herbage mass (see also Thornley, 1998). Using equation 2.8, the current model does not show any discontinuities, yet shows the same phenomena, i.e. a high total animal intake and low stability at intermediate levels of the maximum intake rate.

Empirical responses of total intake to maximum grazing rate are well documented (e.g. Curll *et al.*, 1985a), and generally show an optimum stocking level at which total animal intake (or growth) is maximal. However, no long-term data were available on the response of the system stability to stocking density, as the duration of stocking rate experiments rarely exceeds three successive years. Some evidence for the effectiveness of escape mechanisms is given by Evans *et al.* (1992), who studied clover varieties differing in leaf size under various management regimes. Under continuous sheep grazing, and low herbage masses, small leaved clover varieties were far

more persistent than the large leaved varieties.

*2.2.9 Selective grazing*

Selective grazing of animals entails the discrepancy between the botanical composition of the sward and that of the diet ingested. This is a complex area, as it involves both within-species selectivity for lamina tissue over sheath and stem tissue (Brereton & McGilloway, 1999), and between-species selectivity for a particular species (e.g. Milne *et al.*, 1982; Grant *et al.*, 1985; Binnie & Chestnutt, 1994). It is important to discriminate "apparent" selectivity from "real" selectivity: apparent selectivity may simply arise when the botanical composition of the grazed sward stratum differs from the composition of the entire sward (Milne *et al.*, 1982). Real selectivity involves the intrinsic preference hierarchy of animals for particular plant species. However, this preference may be limited by the total herbage mass, the horizontal and vertical species distribution, as well as by animal factors such as handling time and searching time. Assuming that animals attempt to optimise their daily energy and nutrient balances, their intrinsic preferences may be compromised by the need to maximise their daily intake (Parsons *et al.*, 1994).

Although spatially explicit models, such as presented by Parsons *et al.* (1994), are required to simulate the extent and effects of selectivity satisfactorily, here Schwinning & Parsons' approach (1996a) is followed and expanded. They attributed fixed fractional preferences of 0.3 and 0.7 to grass and clover, respectively. Here, the fractional preferences of 0.5 for both species, used in equations 2.7 and 2.8, are replaced by the parameters $f_1$ and $f_2$ for grass and clover, respectively. The intake of either species is then given by:

$$g_1 = g_{max} \cdot \frac{H_1^{q_{esc1}}}{H_1^{q_{esc1}} + k_g^{q_{esc1}}} \cdot \left(1 - f_2 \frac{H_2^{q_{esc2}}}{H_2^{q_{esc2}} + k_g^{q_{esc2}}}\right) \qquad \text{Eq. 2.9a}$$

$$g_2 = g_{max} \cdot \frac{H_2^{q_{esc2}}}{H_2^{q_{esc2}} + k_g^{q_{esc2}}} \cdot \left(1 - f_1 \frac{H_1^{q_{esc1}}}{H_1^{q_{esc1}} + k_g^{q_{esc1}}}\right) \qquad \text{Eq. 2.9b}$$

Figure 2.10 shows that a fractional preference for clover of 0.7 (default value) has a destabilising effect on the grassland system (compare Figure 2.10a with Figure 2.8a). Conversely, if the preference would have been reversed in favour of perennial ryegrass, this would stabilise the system into a stable, non-oscillating mixture (compare Figure 2.10b with Figure 2.8b).

Field observations show a larger extent of selective grazing by sheep than by cattle, both in grass-clover mixtures (e.g. Evans *et al.*, 1992) and in multi-species mixtures, in which sheep showed

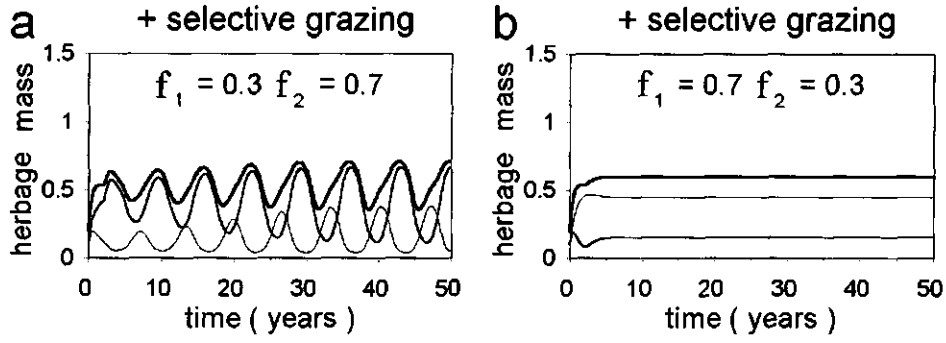


Figure 2.10: The effects of selective grazing on the herbage masses of grass and clover under a) 70% and b) 30% clover preference. Legend as in Figure 2.2.

a stronger between-species preference for forbs and a stronger within-species preference for life tissue, which is possibly related to the smaller mouth areas of sheep (Grant *et al.*, 1985). Evans *et al.* (1992) tested the performance of five clover varieties with different leaf sizes under continuous grazing by sheep, under rotational grazing by sheep and by cattle, and under a cutting regime. He found that none but the small-leaved varieties were persistent under continuous grazing by sheep during a three-year period. The persistence of all varieties was found to increase progressively when they were instead managed under regimes of rotational sheep grazing, rotational cattle grazing, and cutting.

Finally, the interaction between grazing pressure, escape mechanisms, selective grazing, and time is highly complex. Where diet composition is initially the result of spatial availability, total herbage mass, and animal preference, over time it is progressively more dependent on the turnover rates of the grassland species. Eventually a clover-rich diet may only be sustained if clover has a higher growth rate under the present sward conditions (Parsons *et al.*, 1991b; Schwinning & Parsons 1996a). This may lead to paradoxes, where an increased preference for clover may eventually lead to a smaller herbage and clover intake (paradox of imprudence), as shown by the data of Evans *et al.* (1992), mentioned above.

The complexity of the interactions between grazing pressure, escape, and selectivity are exemplified in Figure 2.11, where the average clover content of the sward, the average total intake, and the average system variability (quantified in Chapter 3) over a 50-year time period are presented for a wide range of maximum intake rates (stocking rates), animal preferences for clover, and escape mechanisms for clover.

In spite of the simplicity of the current model, Figure 2.11 shows at least qualitatively how selective grazing, and its interaction with the maximum intake rate and escape mechanisms, has a

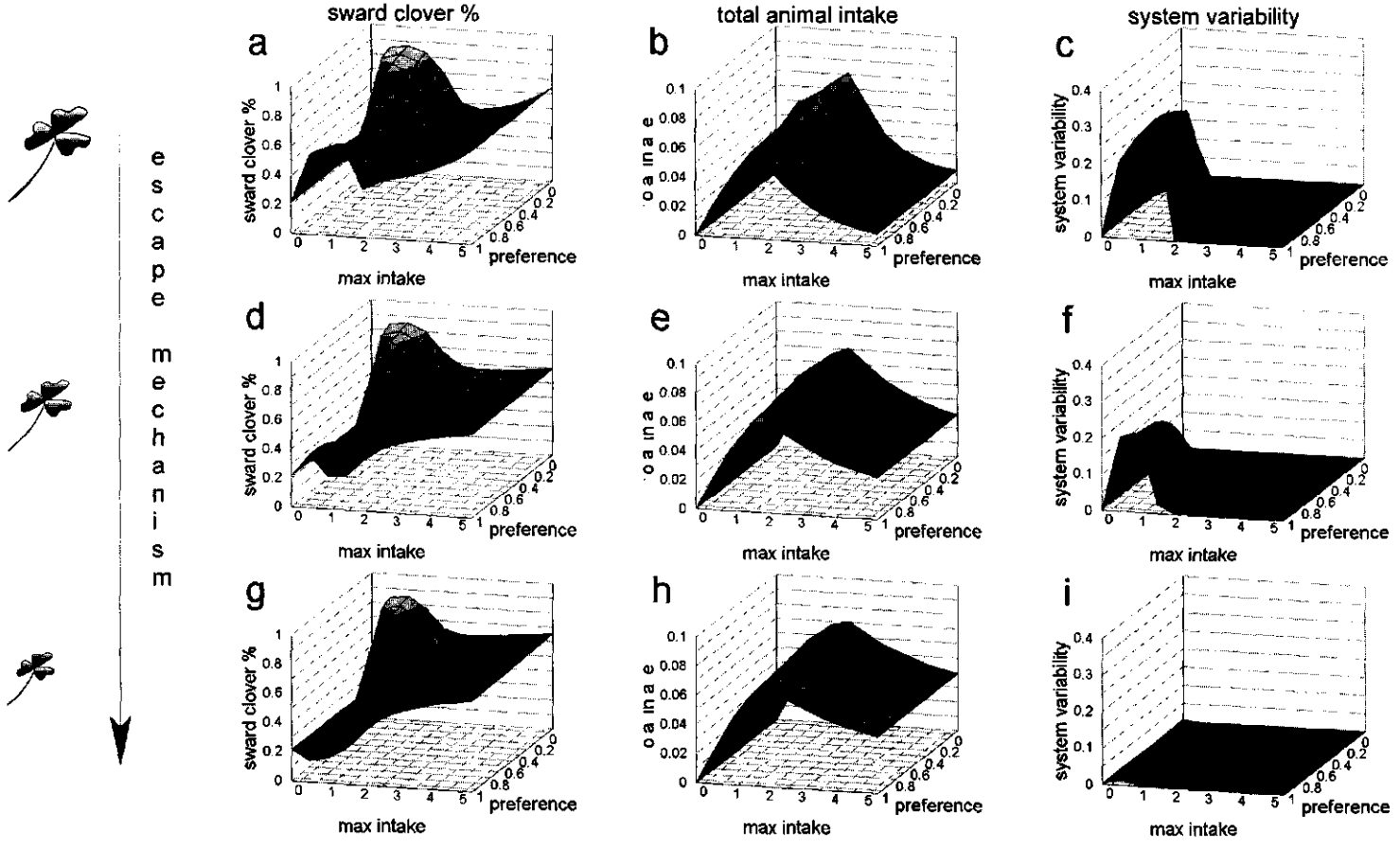


Figure 2.11: Interactions between maximum intake, preference for clover, and escape mechanisms for clover. Figures a, b, c: weak escape mechanism for clover ($q_{esc2} = 1.5$); figures d, e, f: medium escape ($q_{esc2} = 2$); figures g, h, i: strong escape ($q_{esc2} = 2.5$). Effect on a, d, g: average clover content of the sward; b, e, h: average total gross animal intake; c, f, i: system variability.

decisive impact on the average clover content of the sward. At the default settings of the grazing parameters ($g_{max} = 1$, $q_{esc1} = q_{esc2} = 2$, $f_2 = 0.7$; left front corner of Figure 2.11d), the average clover content of the sward is close to its minimum, whereas it accumulates with an increasing maximum intake rate. The latter is caused by the progressively reduced herbage mass at higher stocking rates, reducing both clover and grass growth. However, as this also reduces nitrogen fixation (Ryle *et al.*, 1989) and availability, grass growth is not only compromised by grazing, but also by a limited nitrogen supply. Moreover, Schwinning & Parsons (1996a) found that higher stocking rates lead to an accelerated concentration of nitrogen in urine and manure patches, and therefore to a nitrogen depletion at field scale, creating favourable conditions for clover growth.

Total animal intake appears nearly insensitive to clover preference, which is again in line with Schwinning & Parsons (1996a) (their Figure 10 d, e, f). However, total intake shows the same single maximum response to the stocking rate as earlier observed in Figure 2.9.

Most strikingly, Figure 2.11f reveals that at the default parameter settings, the ecosystem shows a high variability of production. Both an increase in stocking density or a decrease in clover preference would stabilise the system into a stable mixture. Alternatively, a stronger escape mechanism for clover ($q_{esc2} = 2.5$, Figure 2.11i) would stabilise the system for all stocking rates and preferences, which explains the higher persistency of small-leaved clover varieties under continuous sheep grazing (Evans *et al.*, 1992). Note that this stronger escape mechanism does not affect total animal intake at low stocking densities, even though it leads to a somewhat lower clover content in the sward (compare Figures 2.11d and e with 2.11g and h). Conversely, a weaker escape mechanism for clover increases the sward clover content at low stocking densities, yet does not affect the total animal intake. Nevertheless it leads tot an increased instability of the system over time (Figures 2.11a, b, c).

The variety of responses to grazing observed here, could possibly offer an explanation for the often conflicting results from field experiments. Whereas Curll *et al.* (1985a) found a negative relationship between stocking rate and clover content, both Orr *et al.* (1990) and Parsons *et al.* (1991a) reported on an experiment in which higher clover contents were found on swards grazed "hard" at 3 cm than on swards grazed "lenient" at 6 or 9 cm. Both experiments involved continuous grazing by sheep. However, Curll *et al.* used the large-leaved clover cultivar *Blanca*, whereas the small-leaved cultivar *Huia* was used in the other experiment. If Figure 2.11a represents large-leaved clover, with a weak escape mechanism due to its erect morphology, it shows that the average clover content decreases with stocking rate for at least a range of low stocking rates (look for negative slope). However, the clover content is positively related to the stocking rate, for *all* stocking rates in Figure 2.11g, representing small-leaved clover with a prostrate morphology.

## 2.3 Effects of scale and disturbances

*2.3.1 Effect of spatial scale*

So far the intrinsic ecosystem properties have implicitly been modelled in absence of spatial heterogeneity and external disturbances. These simulations represent the processes on a patch-scale, i.e. on a spatial scale at which the herbage of each species may be assumed to be distributed homogeneously, and at which all individuals of one species hence may be assumed to show identical responses over time. However, the stability of a system depends to a large extent on the scale on which it is studied (Collins, 1995). The interaction between the dynamics on a patch scale and on field scale have been explored extensively by Schwinning & Parsons (1996b), using a spatially explicit model, which allowed for the heterogeneity and the active interaction between patches. They concluded that systems which show oscillating yields on a patch scale, may turn into stable mixtures when studied on field scale, provided that the patches oscillate "out of phase".

In the previous section it has been shown how individual patches may be stabilised by increased niche-differentiation, dependence of grass on clover, and management. However, using the default parameter values, representing continuous grazing under the low stocking rates commonly applied on clover-driven pastures, the system shows oscillating behaviour on a patch scale. The same results were found by Schwinning & Parsons (1996a). Setting these patches out of phase may provide an additional management tool to ensure stability at field level.

Schwinning & Parsons (1996b) distinguished four types of patches, based on the relative contributions of grass and clover, and on the soil mineral nitrogen status: 1) clover dominance, 2) grass dominance, 3) pure grass at high soil N, and 4) pure grass at low soil N. When all patches show oscillatory behaviour, the clover dominant phase and the grass dominant phase alternate on each patch. When local clover extinctions and invasions are included, patches may in time move through all four phases periodically and irregularly. The authors came to the conclusion that the "patchiness" of pastures, which occurs when patches are out of phase, is a desirable feature in the maintenance of the stability of pastures, in other words: spatial and temporal heterogeneity on a small scale leads to stability on a large scale.

Strikingly, the same observation was made by Oldeman (1990), studying forest ecosystems. He stated that it is the fluidity of the eco-unit (patch) development itself that guarantees the inflexibility of their mosaic (pasture), because interaction between eco-units (patches) is open and erases the effects of small or somewhat larger diversifying forces.

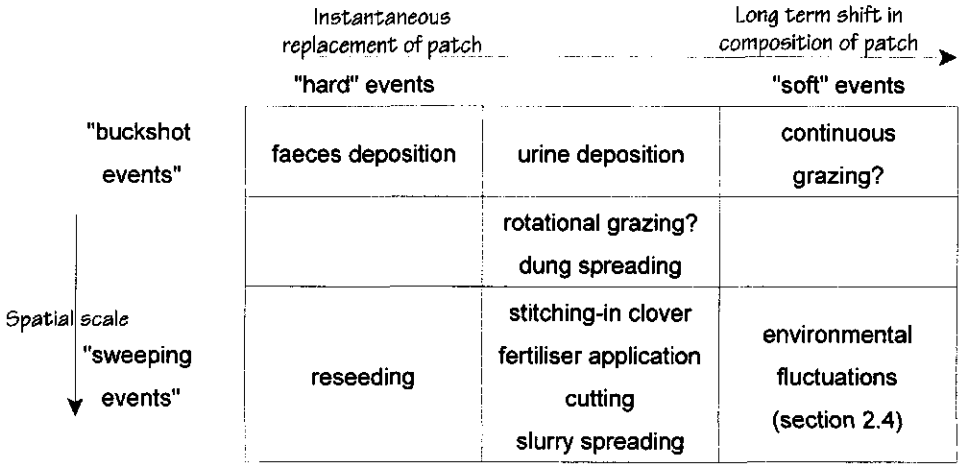


Figure 2.12: Two-dimensional categorisation of disturbances in grassland. For explanation see text.

*2.3.2 Effect of disturbances*

Oscillating patches may be set either "in phase" or "out of phase" by "disturbances", depending on the spatial scale of these disturbances. Small and frequent local disturbances, such as faeces and urine deposition and local tissue removal by grazing animals, are destabilising on a patch scale (Schwinning & Parsons, 1996b). Nevertheless, these set the patches out of phase, and are therefore stabilising on a field scale. These disturbances will here be referred to, *sensu* Oldeman (1990) as "buckshot events". Large-scale disturbances, such as reseeding, the stitching-in of clover, and environmental disturbances (see section 2.4), affect all patches in an identical manner, and are therefore destabilising on a field scale. These large-scale disturbances will be referred to, again *sensu* Oldeman (1990), as "sweeping events". Disturbances may also be classified on a scale of "hardness". "Hard" disturbances, such as faeces deposition and reseeding, instantly mark the end of an existing patch or of multiple patches, and the start of new patches with changed properties. "Soft" disturbances, such as urine depositions (in absence of urine scorch) or a cutting event, may change the patch properties over a time period, as they affect its properties in a more subtle way, e.g. by changing the soil mineral nitrogen balance (Curll, 1982). Figure 2.12 summarises this two-dimensional classification of disturbances.

The positions of continuous and rotational grazing in this figure are questionable: continuous grazing will lead to lower instantaneous stocking rates, and hence to a small and infrequent "buckshot" grazing of each patch. Under rotational grazing all neighbouring patches will be grazed harder and more equally instead. On the other hand, the lower instantaneous stocking rate under continuous grazing may enable the grazing animals to exploit their preference (Figure 2.11). It is conceivable that this may result in a uniform clover removal among all patches (Curll, 1982).

If a pasture is fluctuating on a patch scale, yet stabilised on a field scale by the occurrence of buckshot events, which set the patches out of phase, then it is doubtful whether this situation can still be referred to as a "steady state". Oldeman (1990) proposed the term ecuilibrium (from eco-equilibrium) to describe situations where forest ecosystems are stabilised by fluctuations and disturbances on a small scale, and this seems to be equally applicable to grassland ecosystems:

> the proportions of eco-units (patches) have reached an equilibrium with the local regime of shifting events (disturbances).The existence of an ecuilibrium stage presupposes that there is a regular regime of shifting events (disturbances) (...) Not only is this rarely taken into account in forest (pasture) management plans, but (moreover) vegetation types, including forest (pasture) types, are correlated with average, long-term climatological features only (Oldeman, 1990).

For a more detailed account of the effect of disturbances on patches and field scale, see Schwinning & Parsons (1996b).

## 2.4 The effect of structured and stochastic environmental variability

### *2.4.1 Structured vs. stochastic variability*

So far the stabilising and destabilising factors have been identified in a constant environment. In temperate climates however, "real" grassland ecosystems are confronted with alternating favourable and unfavourable environmental conditions. Temperature and precipitation are the two most obvious variables regulating plant growth (but see Thornley, 1998). Most environmental variables show a seasonal trend, which is to some extent perturbed by stochastic variation (Figure 2.13). The magnitude of both this trend and of the stochastic variation may vary between climates and between variables: whereas temperature shows a strong seasonal trend with relatively small random variations in most temperate climates, rainfall tends to show a stronger stochastic pattern in comparison to its seasonal trend. Figures 2.13a and 2.13b illustrate the fluctuations of temperature and rainfall measured in Wageningen, The Netherlands. Barthram *et al.* (1992) presented similar graphs for central Scotland (their Figure 1). It will be shown here how structured (seasonal) variation and stochastic variation have different impacts on the stability of grassland ecosystems.

### *2.4.2 Impact of structured environmental variability*

The seasonal trends of temperature and rainfall are given by their daily, weekly, or monthly values, averaged over a large number of years. The structured variation can then be quantified by the variance among these average values. The seasonal trend and its variance are constant between

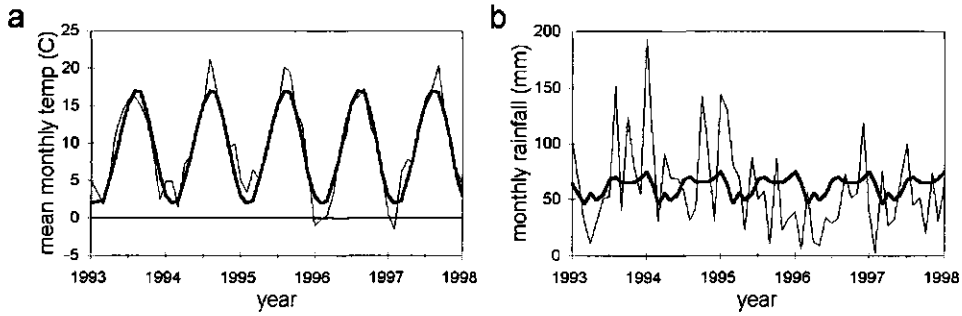


Figure 2.13: a) temperature and b) rainfall patterns in Wageningen, The Netherlands, from 1993 to 1997. Single lines: monthly average values, bold lines: monthly values, averaged over 40 years. Data from the Dept. of Meteorology and Air Quality, Wageningen University, The Netherlands.

years for any particular climate (ignoring possible climate changes).

First the effects of temperature fluctuations on the stability of grass and clover growth will be explored, whereas all other environmental variables (e.g. rainfall, radiation) are assumed to remain constant. The structured seasonal trend of the temperature $T$ is, *sensu* Thornley (1998), modelled as:

$$T = 1 + a_{struc} \cdot \sin(2\pi \cdot t) \qquad \text{Eq. 2.10}$$

where $t$ is the time in years, and $a_{struc}$ the amplitude of the structured fluctuations. Note that the average temperature equals 1 unit, which is the (constant) value implicitly used in the constant environment of section 2.2.

The effect of temperature on the $CO_2$ assimilation rates of perennial ryegrass and clover leaves was documented by Woledge & Dennis (1982), who found a non-linear relationship for both species. The responses of the $CO_2$ assimilation rates to temperature were also affected by the light intensity and by the temperature at which the plants had grown previously. No major differences were observed between the responses of grass and clover. Ignoring light intensities and previous temperatures, the effect of the temperature on the growth of both species is here modelled as:

$$p'_1 = p_1 \cdot T^{q_{temp1}} \qquad \text{Eq. 2.11a}$$

$$p'_2 = p_2 \cdot T^{q_{temp2}} \qquad \text{Eq. 2.11b}$$

where $p'_1$ and $p'_2$ are the temperature dependent growth rates, $p_1$ and $p_2$ are the temperature

independent growth rates of equations 2.6 and 2.4b, respectively, and $q_{temp1}$ and $q_{temp2}$ are parameters indicating the linearity of the response of the photosynthesis to the temperature. These functions ensure that the production of both species equals 0 when the temperature is zero, and that the production is unaffected when the temperature is 1, for all values of $q_{temp}$ (Figure 2.14). For the default values of $q_{temp1}$ and $q_{temp2}$ (0.3 for both species), the responses agree well with the temperature responses found by Woledge & Dennis (1982) under high light intensities.

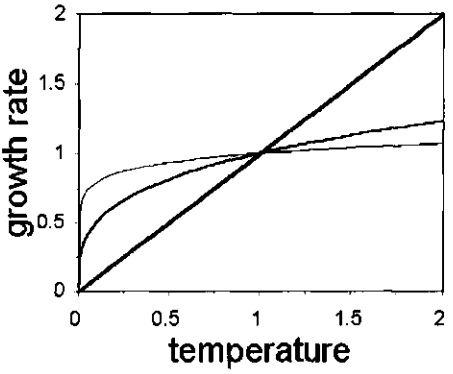


Figure 2.14: response of the growth rate to temperature for $p_i = 1$. Thin line: $q_{tem} = 0.1$, single line $q_{tem} = 0.3$ (default), bold line: $q_{tem} = 1$.

The senescence rate is also dependent on the temperature, which is modelled here as a linear relationship, *sensu* Johnson & Thornley (1983) :

$$s'_i = s_i \cdot T \qquad \text{Eq. 2.12}$$

where $s'_i$ is the temperature dependent senescence rate of grass ($i = 1$) and clover ($i = 2$), and $s_i$ the independent rate. Again the senescence rate equals 0 when the temperature is zero, and is unaffected at the average temperature of 1. Note that a minimum level of 0 has been applied to both production and senescence of both species to prevent negative growth and senescence rates at temperatures below zero ($T < 0$), which would otherwise arise in case $a_{struc} > 1$.

The effect of structured environmental fluctuations on two of the modelled grassland ecosystems is studied: 1) an intrinsically unstable system, showing sustained oscillations in a constant environment. This system is simulated by setting all parameters at their default values. 2) An intrinsically stable system, which is obtained at default parameter settings, yet without the time delay of the dependence of grass on clover ($\tau_{delay} = 0$ in equation 2.6).

Figure 2.15 shows the effect of the structured variation of temperature (equation 2.10) on the stability of the intrinsically unstable system. In absence of these fluctuations, the total herbage mass shows sustained oscillations (Figure 2.15a). Obviously, the seasonal temperature fluctuations lead to a strong variability of the herbage mass *within the year*, the intra-annual variation (Figure

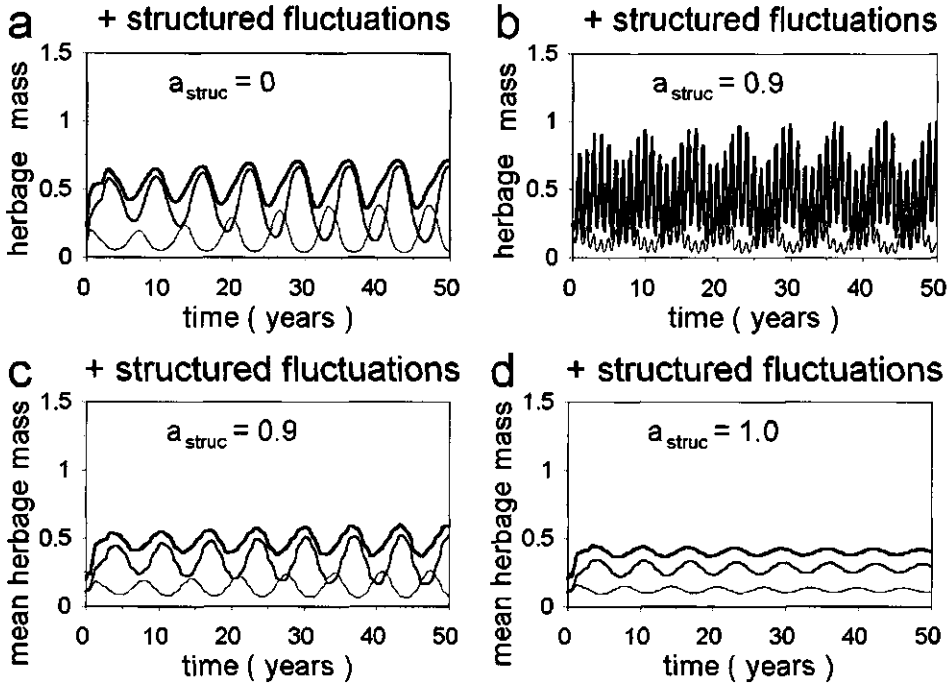


Figure 2.15: Effects of structured environmental fluctuations on the stability of the ecosystem. *a*: $a_{struc}$= 0 (no fluctuations); *b* and *c*: $a_{struc}$ = 0.9; *d*: $a_{struc}$ = 1.0. In *a* and *b* the instantaneous herbage masses are plotted, in *c* and *d* the progressive annual mean herbage masses. Legend as in Figure 2.2.

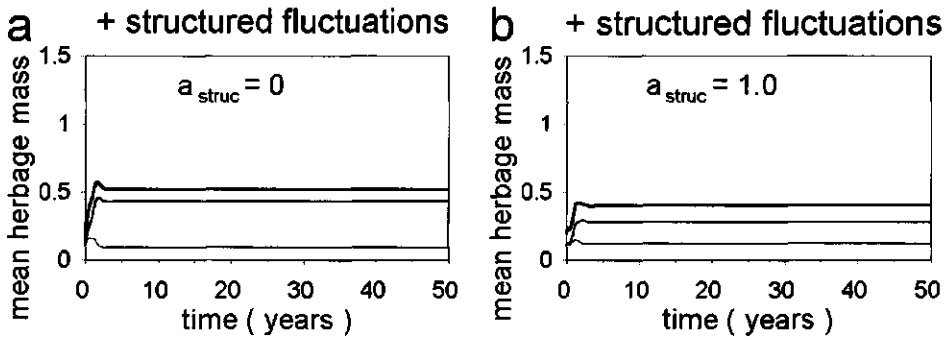


Figure 2.16: Effects of structured fluctuations on a non-oscillating system. *a*: $a_{struc}$ = 0 (no fluctuations), *b*: $a_{struc}$ = 1. Legend as in figure 2.2.

2.15b). This will be referred to as the *direct effect* of the temperature on the system stability. However, when the progressive yearly average herbage mass is plotted over time, it shows that the variation *between years*, i.e. the inter-annual variation, is effectively reduced when large structured fluctuations are imposed (Figures 2.15c and 2.15d). This will be referred to as the *indirect effect* of

the temperature fluctuations.

Figure 2.16 shows the indirect effect of structured temperature variation on the intrinsically stable grass clover mixture. This system remains stable, as the mean yearly temperature is constant and equals 1 for each year. However, the annual mean herbage mass is reduced, as a result of the non-linear response of plant growth to temperature. This disables the extra growth at temperatures $> 1$ to compensate for the reduced growth at temperatures $< 1$ (Figure 2.14).

*2.4.3 Impact of stochastic environmental variability*

To simulate the impact of stochastic variability of an environmental variable, the temperature $T$ in equation 2.10 is now replaced by:

$$T = 1 + a_{stoch} \qquad \text{Eq. 2.13}$$

where $a_{stoch}$ is a random number between $a_{stoch,\,max}$ and $-a_{stoch,\,max}$, which sets the upper and the lower limits of the amplitudes of the stochastic variability.

Figure 2.17 shows that the response of an intrinsically unstable system may now be rather unpredictable, even when $a_{stoch,\,max}$ remains unchanged. In Figure 2.17a, the system is destabilised by the stochastic temperature pattern (compare with Figure 2.15a). However, when the model is rerun for the same parameter values, changing the timing of individual high and low stochastic fluctuations yet for the same value of $a_{stoch,\,max}$, the system may be stabilised (Figure 2.17b). Apparently the times at which high and low temperatures occur is critical in magnifying or counteracting the intrinsic oscillations.

The system which is intrinsically stable (Figure 2.16a) is destabilised by stochastic fluctuations (Figure 2.18). This is caused by the mean annual temperature which is no longer constant, but instead changes from year to year, depending on the stochastic temperature regime.

Similar effects of structured and stochastic environmental fluctuations were observed by Schwinning & Parsons (1996b): system oscillations in their model were reduced when a fixed mortality rate was imposed on clover each winter. Contrastingly, variable winter mortality rates led to sustained oscillations.

*2.4.4 Impact of both structured and stochastic environmental variability*

As discussed above, environmental fluctuations will generally consist of both a structured (seasonal) and a stochastic (daily, weekly or monthly) component. It is assumed here that these two

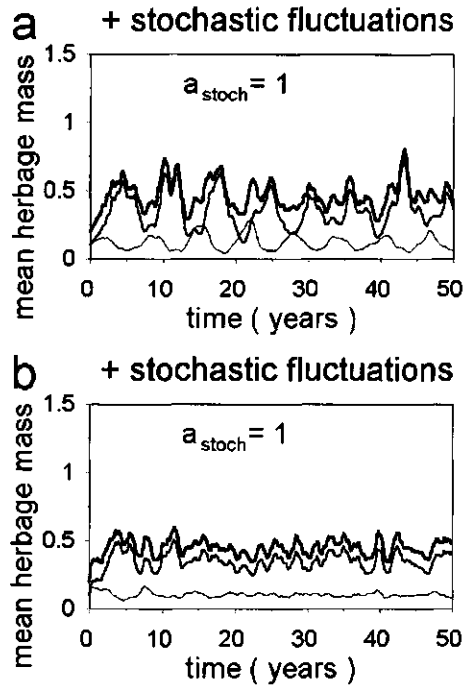


Figure 2.17: Effects of stochastic fluctuations on an oscillating system. a & b: two consequent model runs with identical parameter values. Legend as in fig 2.2.

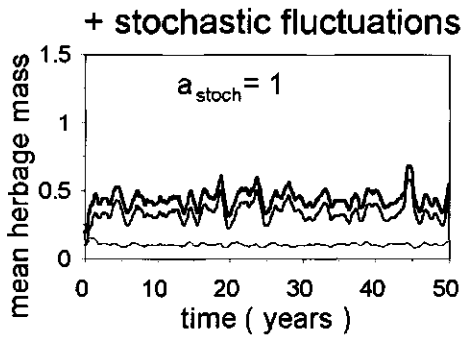


Figure 2.18: Effects of stochastic fluctuations on a non- oscillating system. Legend as in fig 2.2.

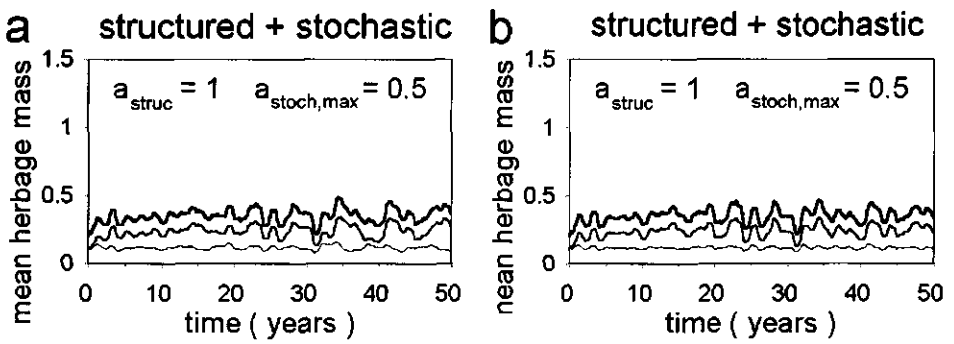


Figure 2.19: Effects of both structured and stochastic fluctuations on a: an intrinsically oscillating system and b: an intrinsically stable system. Legend as in figure 2.2.

components do not show any interaction, i.e.: the daily stochastic variation is as large in winter as it is in summer. The temperature $T$ can then be simulated by adding both components (equations 2.10 and 2.13):

$$T = 1 + a_{struc} \cdot \sin(2\pi \cdot t) + a_{stoch} \qquad \text{Eq. 2.14}$$

Figure 2.19 presents the effect of a large structural component ($a_{struc} = 1$) and a moderate stochastic component ($a_{stoch,\ max} = 0.5$) on the stability of both an intrinsically oscillating system (Figure 2.19a) and an intrinsically stable system (Figure 2.19b). The regime of stochastic fluctuations was kept identical for both systems. Now the identical behaviour of both systems over time is remarkable ( $R^2 = 0.98$), considering the largely contrasting behaviours of these systems under constant average environmental conditions. This underlines the importance of including both structured and stochastic environmental fluctuations into simulation models, in order to predict realistic results. In Chapter 4 it will be shown that this identical behaviour of contrasting systems can also be found in empirical field data.

## 2.5 Classification of stability

Most theoretical ecosystem studies have focussed implicitly on the stability of ecosystems under constant environmental conditions (e.g. Noy-Meir, 1975; Grenfell, 1988; Parsons *et al.*, 1991b; Parsons *et al*, 1994). At most, sinusoidal environmental fluctuations are implemented (e.g. Thornley, 1998), and in nearly all studies stochastic fluctuations are ignored, as these "obscure" the intrinsic ecosystem properties. However, it has been shown in the previous section how both structured and stochastic fluctuations may have a profound impact on the stability of grassland ecosystems. Including the effects of these fluctuations in a qualification and quantification of system stability may be a prerequisite for applicability for both farmers and agronomists.

In contrast, in most empirical studies an attempt is made to explain yield differences between years by the variability of environmental factors. It is interesting to note that yields are commonly linked to rainfall (e.g. Barthram *et al.*, 1992; Silvertown & Dodd, 1994), which is an environmental variable with a strong stochastic component. Its stochastic nature causes variability of rainfall between years, making rainfall an obvious candidate to explain yield differences between years. The effects of temperature are commonly ignored, as its fluctuations are strongly structured, leading to a constant mean yearly temperature between years. Nevertheless it has been demonstrated in section 2.4, that in spite of this constant mean yearly value, structured fluctuations of temperature within years may have a large impact on the system stability between years.

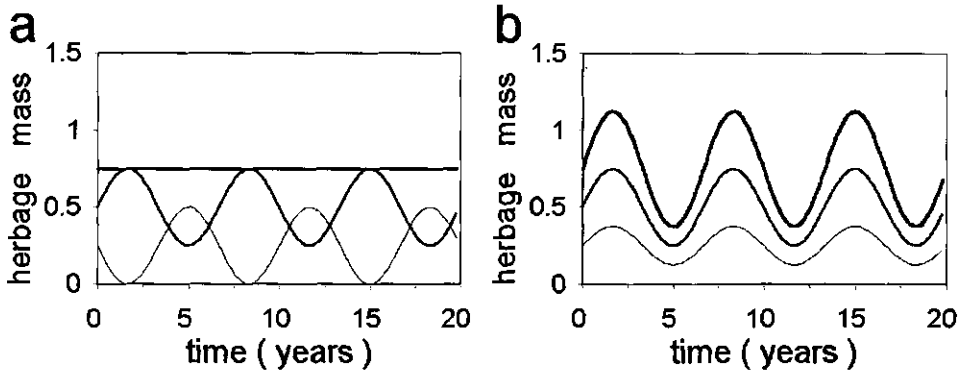


Figure 2.20: Hypothetical inverse relationships between the stabilities of clover content and total herbage mass. a: oscillating clover content, stable herbage mass, b: stable clover content (33%), oscillating herbage mass. Thin line: clover herbage mass; single line: grass herbage mass; bold line: total herbage mass.

In this section an attempt is made to come to a classification of grassland stability which allows for the effects of both intrinsic system properties and for the effects of structured and stochastic environmental variability. First, output variables are identified which represent the entire ecosystem, and the dynamics of which could serve as indicators of system stability. Next, both the spatial scale and the temporal scale at which these variables should be studied are defined. Finally, three concepts of ecosystem stability are proposed.

*2.5.1 Identification of relevant variable*

It is essential to identify an output variable of the system which represents the entire system, yet is also of direct importance to farmers. Noy-Meir (1975) found that the total herbage mass was a more reliable indicator of system stability than was total animal intake and performance, as the latter may be high even when the system is on the verge of a collapse. Total herbage mass, or related variables such as the total Leaf Area Index, are also used by other authors (e.g. Parsons *et al.*, 1991b; Schwinning & Parsons, 1996b; Thornley 1998), as the total herbage mass is the central state variable of most grassland models. However, three limitations in its use should be kept in mind: firstly, there is a tendency to base pasture rotations on "sward surface heights" (e.g. Bircham & Hodgson, 1983; Orr *et al.*, 1990; Evans, 1992; Laws & Newton, 1992), rather than using "fixed rotations" (e.g. Curll *et al.*, 1985a). The sward surface height is strongly related to herbage mass. Whenever this management type is applied, the stability of the herbage mass may depend primarily on the farmer's skills to maintain the desirable height, rather than on system or environmental properties. Secondly, when the stability is studied in conjunction with production, herbage mass may be a poor indicator of agronomic productivity; e.g. understocking will lead to higher total herbage

masses, whereas it may result in a lower total animal production. Finally, cutting grassland for conservation will cause a variable herbage mass within the year regardless of the system's stability properties. In these cases the annual yield, the annual production, or total annual animal intake may be more appropriate output variables, bearing in mind their restrictions mentioned above.

In some studies the clover content, expressed as a percentage of the total herbage mass is used to study the system stability (e.g. Laws & Newton, 1992; Schwinning & Parsons, 1996b). However, care should be taken in this approach, as a fluctuating clover content does not necessarily lead to a fluctuating herbage mass (e.g. Figure 2.20a), nor does a constant clover content implicitly indicate system stability (e.g. Figure 2.20b).

*2.5.2 Identification of relevant spatial scale*

It has been laid out in section 2.3, that a satisfactory study of system stability requires a spatial dimension beyond the patch size, as spatial scale may have a definite impact on system stability. Ideally, the stability of production at farm level should be the focus of attention (e.g. Laws & Newton, 1992), as this is the scale at which farmers operate. It is conceivable that wherever regular reseeding is required to maintain pasture productivity, resulting in oscillating pastures (section 2.3), that stability *at farm level* may be maintained by setting these entire pastures "out of phase". Alternatively, a stable animal production may be achieved from unstable pastures by increasing the conservation and outdoor feeding of herbage.

*2.5.3 Identification of relevant temporal scale*

It is essential to discriminate within-year (intra-annual) stability from between-year (inter-annual) stability. It has been shown in section 2.4 how structured environmental fluctuations will automatically lead to an increased variability of grassland production within individual years, yet may increase stability of production between years. Again, relevance to farmers should be the criterion for the choice: whereas inter-annual stability is arguably most relevant to cattle and sheep producers, the intra-annual stability is just as important to dairy producers. In either case, long-term data are required to provide an indication of stability, as in most short-term data, stability properties are "obscured" by stochastic environmental fluctuations. Moreover, Schwinning & Parsons (1996b) found intrinsic system fluctuations between 4 and 7 years *in the steady state*. In the Park Grass Experiment, botanical equilibrium was not reached until 40 years after the imposement of fertiliser treatments (Silvertown & Dodd, 1994). In an extensification experiment, Wind *et al.* (1993) reported that yields continued to decline for four to seven consequent years after nitrogen treatments ceased in 1968, and that stability of the botanical composition has not yet been reached to date.

*2.5.4 Identification of relevant stability concept*

It has been shown in section 2.4 that both structured and stochastic environmental fluctuations may have a profound impact on the stability of grassland ecosystems. These external factors tend to obscure the intrinsic system properties in field data. This complicates the analysis and comparison of different grassland systems in different climates, measured during different time courses, as the observed output variability may be a reflection of the environmental variability rather than of system properties. To overcome this problem, it is proposed here to define three concepts of stability:

1) *actual stability*: the observed stability of herbage mass, yield or animal intake in an environment showing both structured and stochastic fluctuations. In fact this is the inverse of the variance of yields between years, measured in field experiments. The level of this actual stability is limited to a particular climate and to a particular time period, as it is highly dependent on the (coincidental) stochastic fluctuations during that observation period. A different level may be observed when the same ecosystem is studied under different weather conditions, i.e. at another location, or during another period (e.g. compare Figures 2.17a and 2.17b). Nevertheless, the actual stability level is of direct relevance to farmers.

2) *extrinsic stability*: the observed stability of herbage mass, yield or animal intake in an environment which shows structured yet *no* stochastic fluctuations. The level of this extrinsic stability is limited to a particular system in a particular climate (structured environment), yet remains the same for each observation period (presupposing no change of climate). This means that the extrinsic stability level of an ecosystem (e.g. an experimental plot) will remain constant between distinct observation periods. However, a different level may be expected when an identical ecosystem is studied in another climate (e.g. compare Figure 2.15c and 2.15d). Although the extrinsic stability is independent of the large impact of stochastic environmental fluctuations, at least it incorporates the climate in which the ecosystem is studied.

3) *intrinsic stability*: the observed stability of herbage mass, yield or animal intake in a hypothetical constant environment, as applied in most simulation models. The level of this intrinsic stability is limited only to a particular system, and is identical for all climates and observation periods. This means that ecosystems with identical botanical components, on identical soils, with identical fertiliser and management regimes will show identical levels of intrinsic stability, irrespective of the climate and the period during which it is observed. However, the intrinsic stability level of a grassland ecosystem may profoundly differ from the stability of yields, as measured in the field.

Of these three stability concepts, the actual stability represents most accurately the variance

of yields experienced by farmers. It may be used to compare the short-term stability performance of ecosystems, measured at the same location, during the same time course, e.g. two plots of an experiment. However, it should be kept in mind that the levels of actual stability which are found, may be profoundly different or even be reversed when both ecosystems are observed during a different period, i.e. under a different regime of stochastic fluctuations. Therefore it is proposed here, to use the extrinsic stability levels for these comparisons instead, as these will remain constant over time. In fact, the extrinsic stability could bridge the gap between the stability properties observed in modelled ecosystems, i.e. the intrinsic stability, and those observed in experiments, i.e. the actual stability.

Additionally, a comparison of the actual and the external stability of an ecosystem will reveal its response to the regime of stochastic environmental fluctuations. Similarly, the effect of structured environmental fluctuations can be deduced by a comparison of the external and the intrinsic stability.

When using system simulation models, the extrinsic and the actual stability can be derived from the intrinsic stability relatively simply, by subsequently imposing structured and stochastic environmental fluctuations, as shown in section 2.4. Conversely, the intrinsic and extrinsic stability can be derived from the experimentally measured actual stability. This rather complicated procedure requires large amounts of long term data. This procedure will be explained in Chapter 3.

## 2.6 Discussion

Due to the simplicity of its structure, the model presented in this chapter should not be regarded as explanatory, nor should its predictions be considered conclusive. Quantitative interactions between perennial ryegrass and white clover at patch level have been modelled more satisfactorily by Parsons *et al.* (1991b), Thornley *et al.* (1995) and by Schwinning & Parsons (1996a). However, the higher complexity of their models complicates the discrimination of the effect of individual ecosystem properties and processes, which regulate stability. Contrastingly, the transparency of the model presented here enabled the identification and illustration of the impacts of these individual processes, and of their interactions.

It has been demonstrated that the stability of yields which is observed in the field depends

on a complex of three components: the intrinsic ecosystem properties, the degree of spatial heterogeneity, and on the environmental variability.

Of the intrinsic ecosystem processes, competition for light, delayed responses, grazing *per se*, preferential grazing for clover and cutting were all identified as destabilising, whereas niche-differentiation, nitrogen dependence, and escape mechanism were found to stabilise the ecosystem. To some extent, the stabilising processes may compensate for the instability caused by the destabilising processes. However, interactions between both process types were observed, which complicate this compensation. For instance, a strong clover preference destabilised the modelled ecosystem at low stocking rates, yet did not affect stability at higher animal densities. Moreover, the stability level was independent of clover preference at all stocking rates, when clover was attributed with a stronger escape mechanism (Figure 2.11).

On top of these interactions among intrinsic ecosystem processes, interactions between intrinsic ecosystem processes on the one hand, and spatial heterogeneity on the other, further complicate matters. It was suggested that even when the ecosystem is unstable at a patch scale, it may show a stable level of production at field scale, when the oscillating patches are set "out of phase". Whether patches oscillate "out of phase" or "in phase" depends again on the management imposed. However, the same stability level may be observed when the individual patches are stabilised. Therefore management factors affect the system stability through two pathways, i.e. by changing the balance of intrinsic processes, and by defining the spatial heterogeneity. It was shown, for instance, how preferential grazing under low stocking rates leads to instability at patch scale. At the same time, manure and urine depositions under grazing act as "buckshot" events which increase pasture heterogeneity and therefore stability at field scale.

Finally the picture is further obscured by structured and stochastic environmental fluctuations. It has been argued in section 4.2 that ecosystems which are unstable in temperate climates with small structured fluctuations, may show stable behaviour in more continental climates, in which structured environmental fluctuations are strong. Furthermore, stochastic environmental fluctuations may lead to drastic changes in the stability level between observation periods. Especially in intrinsically unstable systems, the timing of high and low temperatures was found critical to the actual stability level of the ecosystem. Therefore it is well conceivable that an ecosystem which appears to be stable during a five year experiment, would show unstable behaviour when observed at a different date (Figure 2.17). In Chapter 3, it will be demonstrated that when stochastic fluctuations are strong, intrinsically stable systems may in fact show a larger variability of yields than intrinsically unstable systems.

Considering the complexity of all these interactions within and between intrinsic processes, spatial heterogeneity and environmental fluctuations, the prototyping of management systems for

mixed swards is fraud with complications, when based on short-term experiments which establish the system responses to single management factors. In fact this complexity may well explain the large variety of responses of grass and clover to single management factors, as observed in the literature cited. Experimental designs which take all processes and all interactions into account, are hardly conceivable. Chapters 3 and 4 demonstrate how the effect of some single management factors may be extracted from data on long-term experiments, with durations from 40 up to 150 years. However, the number of conclusions contrasts sharply with the huge resources required for these experiments. Therefore the use of simulation models will remain indispensable in the analysis of grassland ecosystem stability.

Bearing in mind the limitations of simulation models mentioned in the introduction, a satisfactory simulation model of mixed swards should incorporate all three components which regulate stability. Primarily it requires an accurate description of the intrinsic system properties and processes, which allows for their mutual interactions. Such a description for grass monocultures has already been presented by Thornley (1998). However, the same level of accuracy and detail has not yet been achieved in models which simulate the intrinsic processes of grass-clover swards (e.g. Parsons *et al.*, 1991b; Thornley *et al.*, 1995; Schwinning & Parsons, 1996a).

Secondly, considering the decisive impact of spatial heterogeneity on system stability at field scale, a simulation model of mixed swards should explicitly locate all processes in a three-dimensional space. This could be achieved by simulating a large number of patches, which all consist of a number of sward layers, and which interact directly with neighbouring patches. Parsons *et al.* (1994) and Schwinning & Parsons (1996b) have already presented two-dimensional (lateral) simulation models of grass and clover under grazing. However, in both models the simulation of intrinsic plant processes was reduced to a most basic level. Brereton & McGilloway (1999) presented a three-dimensional model to study the effects of sward structure on animal intake during short rotational grazing periods. In their model, plant processes were absent, and patches only interacted passively, i.e. through the selection between patches by the grazing animals.

Apart from drastically increasing the number of required calculations, the dynamic simulation of detailed plant processes and of plant-animal interactions in a three-dimensional space would require an adequate description of grass and clover morphology. Morphogenesis of perennial ryegrass was successfully simulated by Van Loo (1993). However, no explicit morpho-physiological models of white-clover were found in the literature.

Finally, in order to produce results which reflect ecosystem behaviour under field conditions, the simulation model should include both structured and stochastic environmental fluctuations. It was demonstrated that even under moderate stochastic fluctuations, the yield patterns of an intrinsically stable and an intrinsically unstable system were nearly identical over time, in spite of the

largely contrasting behaviour of both systems in a constant environment (Figure 2.19). In such cases, the system response to environmental fluctuations makes the balance of all other intrinsic processes nearly irrelevant. Using a model which includes environmental variability, it is conceivable that ecosystems are no longer classified by the intrinsic stability level, but instead by either the extrinsic stability level, or by the probabilities of actual stability levels, e.g. the number of simulation runs in which a range of stability levels were exceeded.

It is envisaged that such a simulation model as described above, combined with data from long-term experiments, could bridge the gap between intrinsic ecosystem properties, which have been revealed by simulation models to date, and actual ecosystem behaviour, as reported from experimental studies. The definitions of the intrinsic, extrinsic, and actual stability levels presented in this chapter, may aid the interpretation of model output in practical terms, and the deduction of intrinsic processes from field data, which would improve the information flows between both approaches. This would not only aid the understanding of grass-clover dynamics, but could also prototype entire management systems for grass-clover mixtures, taking into account all intrinsic, spatial and environmental processes and interactions involved.

## Appendix Chapter 2

Table of state variables, rate variables and parameters used in the model.

| type | symbol | description | introduced in equation: | default value (parameters): |
|---|---|---|---|---|
| time variable | $t$ | time since start of simulation | 2.6 | |
| plant state variable | $H_i$ | Herbage mass | 2.1 | |
| plant rate variables | $p_i$ | Herbage growth rate (temperature independent) | 2.1 | |
| | $p'_i$ | Temperature dependent herbage growth rate | 2.11 | |
| | $s_i$ | Herbage senescence rate (temperature independent) | 2.2 | |
| | $s'_i$ | Temperature dependent herbage senescence rate. | 2.12 | |
| plant parameters | $d_i$ | Relative senescence rate of herbage | 2.2 | 8 (grass), 7 (clover) |
| | $k_{p\,i}$ | Herbage mass at which the growth rate is half-maximal | 2.1 | 0.5 (both species) |
| | $k_{dep}$ | Clover herbage mass at which grass growth rate is half-maximal. | 2.5 | 0.02 |
| | $n_i$ | Fraction of resources of one species, also used by the other species | 2.4 | 1 (grass), 0.9 (clover) |
| | $p_{max\,i}$ | Maximum herbage growth rate | 2.1 | 12 (grass), 9 (clover) |
| | $q_{temp\,i}$ | Parameter controlling the linearity of the growth response to temperature. | 2.11 | 0.3 (both species) |
| | $\tau_{delay}$ | Delay in dependence of grass growth on clover | 2.6 | 2 |

| type | symbol | description | introduced in equation: | default value (parameters): |
|---|---|---|---|---|
| grazing rate variable | $g_i$ | Total intake rate of animals | 2.7 | |
| grazing / cutting parameters | $c_i$ | Fraction of herbage cut annually | - | 0.9 (both species) |
| | $f_i$ | Fractional preference for species by grazing animals | 2.9 | 0.3 (grass), 0.7 (clover) |
| | $g_{max\,i}$ | Maximum total intake rate of all animals | 2.7 | 1 |
| | $k_g$ | Herbage mass at which the total animal intake rate is half-maximal | 2.7 | 0.15 |
| | $q_{esc\,i}$ | Strength of escape mechanism: controls shape of intake response to herbage mass | 2.8 | 2 (both species) |
| environmental variables | $T$ | Temperature | 2.10 | |
| | $a_{stoch}$ | Amplitude of a single stochastic temperature fluctuation | 2.13 | |
| environmental parameters | $a_{struc}$ | Amplitude of structured temperature fluctuations | 2.10 | 0 |
| | $a_{stoch\,max}$ | Maximum amplitude of stochastic temperature fluctuations | - | 0 |

# Chapter 3: A mathematical framework for the quantification of production stability in grassland ecosystems

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## Abstract

1) Mixed grassland ecosystems are characterised by fluctuating yields, caused by a combination of intrinsic system oscillations and environmental fluctuations. The actual stability of a grassland ecosystem is the stability of yields as observed in experiments, where ecosystems are subjected to both seasonal and stochastic environmental fluctuations. The extrinsic stability is defined by the yield stability in an environment which shows seasonal, but no stochastic fluctuations. The intrinsic stability refers to its stability of yields in a hypothetical constant environment.

2) A mathematical framework is presented to deduct the actual, the extrinsic and the intrinsic stability of grassland ecosystems from their yield patterns and the environmental patterns during a long time-course.

3) Intrinsically stable grassland ecosystems remain stable when subjected to structured environmental fluctuations only, yet are destabilised by stochastic environmental fluctuations. However, the sensitivity of stable ecosystems to these stochastic fluctuations is magnified by the structured fluctuations.

4) In temperate climates, intrinsically oscillating grassland ecosystems are on average slightly stabilised by stochastic environmental fluctuations. Structured environmental fluctuations may fully stabilise these systems, when months with temperatures below zero occur on a structural basis, as is the case in continental climates. However, in these climates these ecosystems are destabilised by stochastic environmental fluctuations.

5) It is demonstrated that in environments with large stochastic environmental fluctuations, the actual variability of yields may be lower for an intrinsically oscillating system than for an intrinsically stable system.

6) It is consequently argued that the stability of yields, observed during short-term experiments is a poor reflection of the intrinsic ecosystem properties. Instead, long-term experiments are required to elucidate the relation between these intrinsic properties and the grassland management on the one hand, and the stability of yields on the other.

## 3.1 Introduction

In the previous paper (Chapter 2) the internal and external processes regulating the production stability of mixed grassland ecosystems were reviewed. The intrinsic stability of grassland ecosystems was shown to depend on the sum and the interactions of species characteristics, soil nutrient status, and management. As a result the herbage production of species in grassland mixtures may either be unstable (leading to a stable monoculture), stable, or show damped or sustained oscillations.

Structured environmental fluctuations (i.e. seasonality of e.g. temperature and rainfall) appeared to stabilise intrinsically oscillating ecosystems. The stability of such systems subjected to seasonal climatic fluctuations was defined as the extrinsic stability. Additionally, it was demonstrated that stochastic (i.e. daily or monthly) environmental events may either stabilise or destabilise the ecosystem, depending on the timing of these events in relation to intrinsic system oscillations. The stability of an ecosystem subjected to both structured and stochastic environmental fluctuations, which is in fact the stability measured in field experiments, was consequently defined as the actual stability.

As a result of the dependence of the actual stability level on stochastic environmental fluctuations, it may only be used for a comparison of ecosystems subjected to identical environmental regimes, i.e. two adjacent systems which are measured simultaneously (e.g. two treatments of one experiment). The extrinsic stability depends on the intrinsic system properties, and on the structured environmental fluctuations, but is independent of the noise caused by the stochastic environmental events. Therefore it allows for a comparison of ecosystems which are measured under identical structured environmental fluctuations, yet different stochastic environmental fluctuations, e.g. two treatments of one experiment, observed during different time courses. The extrinsic stability remains constant over time for a particular system in a particular climate, and is hence a more reliable indicator of system stability than the actual stability. Finally, the intrinsic stability is also independent of the environment, and is consequently constant for a particular ecosystem in any given climate. However, considering the large impact of environmental fluctuations on system stability, the intrinsic stability may be a rather poor reflection of the stability of yields, as observed in the field.

Whether using the actual, the extrinsic or the intrinsic stability levels, comparing the stability of ecosystems requires a quantification of stability which is more precise than the qualifications of unstable and stable ecosystems, and of damped oscillations and sustained oscillations, which are frequently found in the literature (e.g. Noy-Meir, 1975; Thornley *et al.*, 1995; Schwinning & Parsons, 1996a,b; Thornley, 1998). No quantification of stability was found, however, other than the variance

of yields among years.

In this paper a quantification is presented of the actual, extrinsic and intrinsic stability of ecosystems, respectively. Using a simulation model, it was demonstrated in the previous paper (Chapter 2) how the extrinsic and actual stability level of an ecosystem can be deducted from its intrinsic stability level. Conversely, it will be shown here how the actual, extrinsic and intrinsic stability of a grassland ecosystem can be consequently deducted from experimental yield data. In the following paper (Chapter 4) this quantification will be exemplified by using data from two long-term grassland experiments in the UK and The Netherlands.

## 3.2 Materials and methods

In the previous paper (Chapter 2) a simple simulation model was presented of a grassland mixture, consisting of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*), under continuous grazing. Throughout this paper, these two species will be referred to as "ryegrass" and "clover", respectively. First, this model was used to study the qualitative response of ecosystem stability to a range of intrinsic processes and system properties. The temporal patterns of the herbage masses of ryegrass and clover, as predicted by the model, were presented in units only, in which one unit corresponded to the maximum herbage mass in the field of a perennial ryegrass monoculture (*sensu* Noy-Meir, 1975). Four types of ecosystems were distinguished: 1) unstable mixtures, leading to stable monocultures, 2) stable mixtures, 3) mixtures in which the herbage mass of both species showed sustained oscillations, and 4) mixtures in which the herbage masses showed damped oscillations, eventually leading to a stable mixture.

Additionally, both structured and stochastic environmental fluctuations were incorporated into the model, by imposing a sinusoidally and a randomly fluctuating temperature, respectively. Two of the ecosystem types were used to study the impact of the structured and the stochastic environmental variability. These were: 1) an intrinsically stable mixture, obtained by setting all model parameters to their default values, apart from the delay between the fixation of nitrogen by clover and its availability to ryegrass, which was set at zero; 2) a system showing sustained intrinsic oscillations, which was obtained by setting all parameters, including the delay, to their default values. The same two types of ecosystems will be used here, to illustrate the quantification of the actual, the extrinsic and the intrinsic stability.

In the previous paper (Chapter 2) it was noted that the simplicity of the model only allowed for a qualitative study and illustration of ecosystem behaviour. Here, the quantitative model

predictions are used to exemplify the quantification of stability. It should be stressed that these model predictions are only used as a "case study". The use of model output was preferred over the use of experimental field data as the former is void of experimental "noise", and hence allows for a more unambiguous illustration of the mathematical framework. The framework will be applied to experimental data in the following paper (Chapter 4).

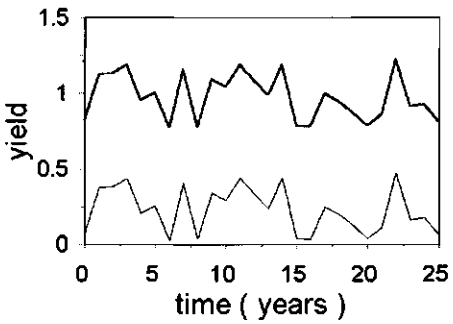


Figure 3.1: Fluctuating yields of two hypothetical grassland ecosystems. Although both systems show equal variances of yields, the system represented by the bold line is more stable (for explanation see text).

## 3.3 Results

### *3.3.1 Stability and variability*

Throughout this paper, the term *variability* is reserved to indicate the inverse of stability. Differences in the stability between ecosystems are quantified as differences in their variability. Hence the actual, the extrinsic and the intrinsic variability indicate the inverses of the actual, extrinsic and intrinsic stability, respectively, while the environmental variability refers to the inverse of the environmental stability.

### *3.3.2 Quantification of the actual stability*

As explained in more detail in the previous paper (Chapter 2), the actual stability of an ecosystem is in fact the stability of yields, or the stability of the annual mean herbage mass, as measured in the field, in the face of both structured and stochastic environmental fluctuations. As a result, the actual variability of a grassland ecosystem is obviously related to the variance of its yields among years. However, this variance represents the absolute magnitude of the fluctuations of yields. Figure 3.1 gives the fluctuating yields of two hypothetical ecosystems, which differ in production level, yet show the same variance of yields. As the *relative* yield differences among years are smaller for the system represented by the bold line, this ecosystem is arguably more reliable and therefore more stable. Consequently, the actual variability of an ecosystem is more accurately represented by the coefficient of variation (CV) of yields among a certain time period, i.e. by the standard deviation divided by the mean yield of the same period:

$$V_{yield\ act} = CV\ (yield) = \frac{s_{yield}}{m_{yield}} \qquad \text{Eq. 3.1}$$

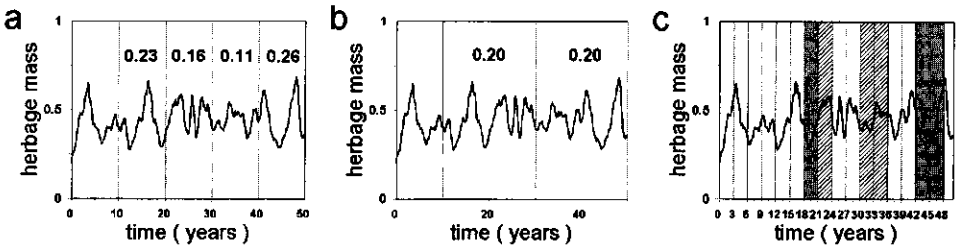


Figure 3.2: Yield pattern and actual variability of an intrinsically oscillating ecosystem. in the face of stochastic fluctuations (Chapter 2: $a_{stoch\ max} = 1$). In a, b, and c the actual variability was calculated for each decade, 20-year period, and 3-year period, respectively. In c, dashed areas indicate periods with low actual variability ($V_{yield\ act} < 0.10$), as these observation periods coincide with the maxima or minima of the intrinsic system oscillations. Shaded areas indicate periods with a high actual variability ($V_{yield\ act} > 0.15$), as these observation periods coincide with intermediate phases of these oscillations.

in which $V_{yield\ act}$ is the actual ecosystem variability, $s_{yield}$ the standard deviation of the yields during the observed time course, and $m_{yield}$ the average yield during the same period. The variable $V_{yield\ act}$ in fact scales the average yearly fluctuation to the average yield. Therefore it has no dimensions and it has a value between 0 and 1 under normal conditions. When yields are identical between years, $V_{yield\ act}$ equals 0, whereas it equals 1 when the average yield fluctuations are as large as the average yield, i.e. when years with no yield alternate with years with a high yield. Only under exceptional circumstances (e.g. a series of years with no yield followed by a single high yield) may its value exceed 1. Since $V_{yield\ act}$ has no dimensions, it is independent of the quantities in which the yield is expressed, be it in g $m^{-2}$, in kg $ha^{-1}$, or in units as in this paper. The actual stability, $S_{yield\ act}$ (no dimensions) is then defined by:

$$S_{yield\ act} = \frac{1}{V_{yield\ act}} \qquad \text{Eq. 3.2}$$

The actual stability may vary over time, depending on the regime of stochastic environmental fluctuations (Chapter 2). This means that periods in which the actual variability of yields is high, are alternated by periods in with a lower variability of yields. This is graphically exemplified in Figure 3.2a. The average yearly herbage mass of the intrinsically oscillating grassland ecosystem is shown for 50 years, as produced by the model in the previous paper (Chapter 2). No structured environmental fluctuations were imposed, whereas stochastic environmental fluctuations were large ($a_{stoch\ max} = 1$).

In Figure 3.2a, the length of the time period over which the actual variability is computed was set at its default value of 10 years. On the one hand, this period is short enough to allow for the expression of changes of the actual stability over time. If a longer time-course would be used instead, this is bound to incorporate both periods with large, and periods with small yield fluctuations (Figure

3.2b). In that case, differences in the actual variability, measured during different time-courses, would become very small.

On the other hand, the 10-year period proposed here is long enough to exceed the periodicity of possible intrinsic system oscillations of 2-7 years (Chapter 2), which have been reported in the literature (Schwinning & Parsons, 1996a; Thornley, 1998; Fothergill *et al.*, 2000). As a result, this 10-year period will incorporate at least one or more of these intrinsic cycles. Therefore, the actual variability is not dependent on the *phase* of the intrinsic oscillations during the observation period. If a shorter time-course would be used instead, the actual variability would be low, when measured during a period in which the yield oscillations are at either their maximum or minimum (dashed periods in Figure 3.2c). Instead, the actual variability would be high when measurements coincide with intermediate phases of the oscillations (shaded periods in Figure 3.2c).

The actual yield variability of the first decade is disregarded, as this is decade incorporates the response period of the ecosystem to a new management or environmental regime. Both in simulated and experimental ecosystems, this response period is frequently associated with a sharp increase or decline of yields or herbage masses from their initial values to their new ecuilibrium values (Chapter 2; see also Wind *et al.*, 1993). This ecuilibrium (from eco-equilibrium: Oldeman, 1990) is the stage in which the magnitude of the yield oscillations do not further increase or decrease in the long term, but instead are a reflection of the intrinsic oscillations and the environmental and management fluctuations only (Chapter 2). Here the actual variability during the response period is disregarded, as it is a reflection of the system's response to the *change* of management or environment, rather than its response to the management or environment itself.

### *3.3.3 Quantification of the extrinsic stability*

The extrinsic ecosystem stability was defined as the stability of yields or the herbage mass in the face of structured, but in the absence of stochastic environmental fluctuations (Chapter 2). By definition, structured fluctuations of e.g. the temperature are identical between years (disregarding possible climate changes). Consequently, structured temperature fluctuations do not lead to differences between the mean yearly temperature values. Instead, these differences are merely the result of the stochastic temperature fluctuations. Therefore, the extrinsic ecosystem variability presumes a stochastic temperature variability equal to zero.

Here the stochastic variability of the temperature between years, $V_{temp\ stoch}$, is defined similarly to the actual yield variability:

$$V_{temp\ stoch} = CV\ (annual\ temp) = \frac{s_{temp}}{m_{temp}} \qquad \text{Eq. 3.3}$$

in which $s_{temp}$ is the standard deviation of the yearly average temperature during a decade, and $m_{temp}$ is the average temperature during this same decade.

Figure 3.3 illustrates the impact of the stochastic environmental variability on the actual yield variability of the intrinsically stable system (Figures 3.3a, b, c) and of the intrinsically oscillating system (Figures 3.3d, e, f), which will be referred to as the intrinsically unstable system.

Each graph in Figure 3.3 was produced by running the simulation model presented in the previous paper (Chapter 2) 50 times for a 50 year time period under a range of stochastic environmental fluctuations (i.e. a range of values for $a_{stoch\,max}$). This resulted in 50 x 4 decades = 200 data points for each graph, as the actual yield variability during the first decade of each run was disregarded. In Figures 3.3a and 3.3d, the model was run in absence of *structured* environmental fluctuations ($a_{struc} = 0$). In Figures 3.3b and 3.3e, these structured fluctuations were imposed with $a_{struc} = 0.9$, and in Figures 3.3c and 3.3f with $a_{struc} = 1$. Additionally the responses of the actual yield variability to the stochastic environmental variability were arbitrarily fitted using the following regression model:

$$V_{yield\ act} = \alpha\ V_{temp\ stoch} + \beta \sqrt{V_{temp\ stoch}} + \gamma \qquad \text{Eq. 3.4}$$

For both systems, the extrinsic yield variability in each climate is now given by the Y-intercept of the regression line ($\gamma$), where $V_{temp\ stoch}$ equals zero. In case field data would be used instead of data produced by simulation models, this intercept can be derived by extrapolation of the actual yield variability.

Figures 3.3a, b, and c show that the intrinsically stable ecosystem is also extrinsically stable for all levels of structured environmental fluctuations (i.e. in all climates), as the intercepts equal zero in all cases. Although the structured environmental fluctuations may cause oscillations of the herbage mass within each year, these oscillations are identical between years. Therefore the average annual herbage mass remains stable between years (Figures 2.16a,b in Chapter 2).

Contrastingly, this ecosystem is progressively destabilised by stochastic environmental fluctuations, as the actual yield variability increases with the stochastic environmental variability.

Figures 3.3d, e, and f present the response of the intrinsically unstable system to the stochastic environmental fluctuations. Again the extrinsic yield variability is given by the Y-intercepts, which are now significantly greater than zero ($p < 0.0001$) for all climates. However, this extrinsic variability is progressively reduced by increasing amplitudes of the structured environmental fluctuations (increasing $a_{struc}$), i.e. in climates with a strong seasonality of the environment (see also Figure 2.15 in Chapter 2).

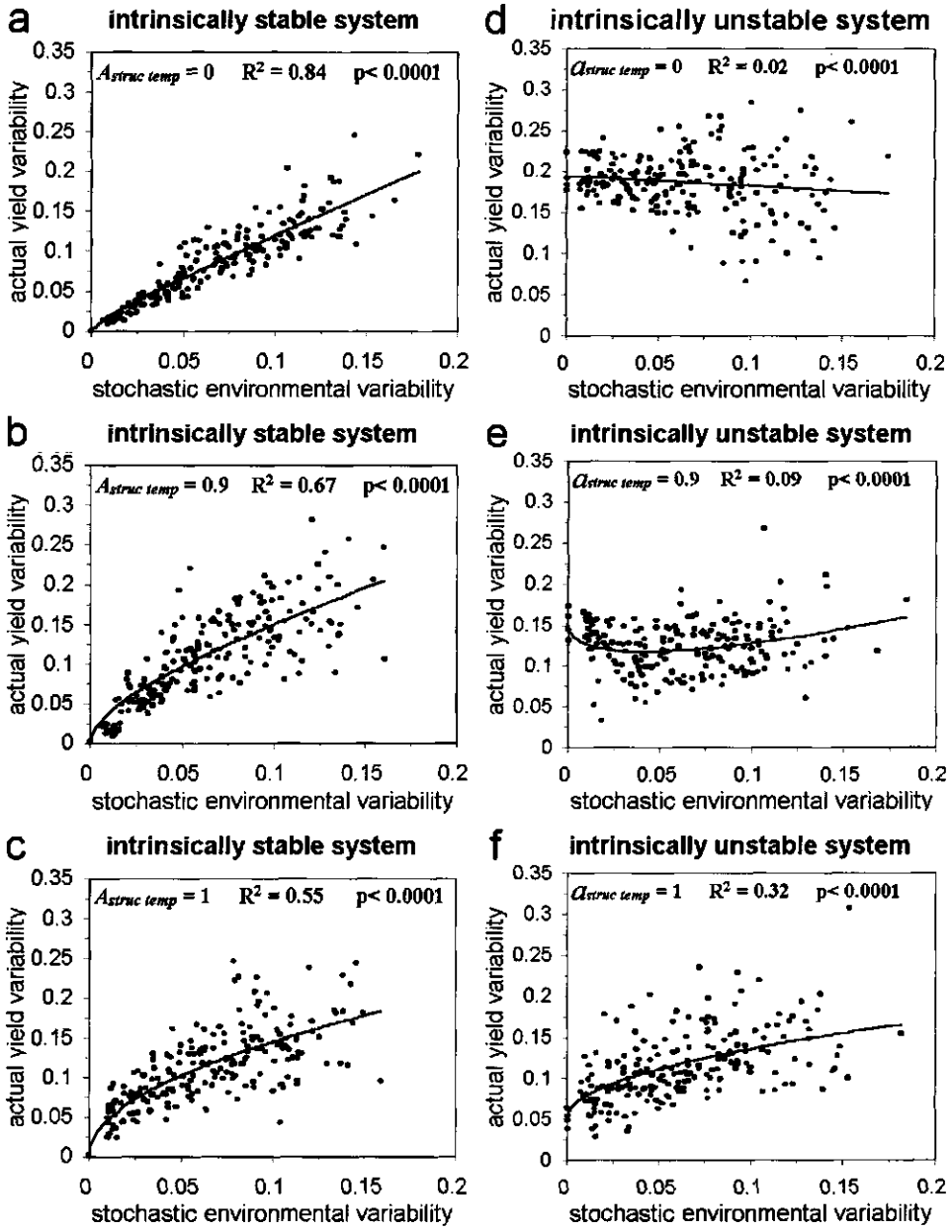


Figure 3.3: Responses of the actual yield variability to the stochastic environmental variability. Figures a, b, and c: intrinsically stable system; d, e, and f: intrinsically unstable system. Figures a and d: no structured environmental fluctuations; b and e: $a_{struc\ temp}$ = 0.9; c and f: $a_{struc\ temp}$ = 1. The extrinsic variability in each graph is given by the Y-intercept.

*3.3.4 Quantification of the intrinsic stability*

The intrinsic yield variability was defined as the yield variability in absence of both stochastic and structured environmental variability. It was shown that the structured environmental variability only leads to herbage mass fluctuations *within* years (Chapter 2). Therefore this structured environmental variability, $V_{temp\ struc}$, is here defined as:

$$V_{temp\ struc} = CV\ (monthly\ temp) = \frac{s_{temp\ monthly}}{m_{temp\ monthly}} \qquad \text{Eq. 3.5}$$

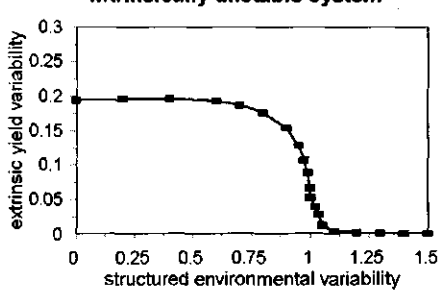


Figure 3.4: Response of the extrinsic yield variability of an unstable ecosystem to structured environmental fluctuations. The ecosystem is unstable in a constant environment (Y-intercept), and is progressively stabilised by increasing structured environmental fluctuations.

in which $s_{temp\ monthly}$ is the standard deviation of the 40-year average temperature of each month, and $m_{temp\ monthly}$ is the average of the 40-year average temperature of each month. The latter in fact equals the average temperature over the entire period. $V_{temp\ struc}$ scales the average monthly temperature deviation to the mean yearly temperature. Hence in temperate climates, in which months with average temperatures below zero do not occur structurally, $V_{temp\ struc}$ will take a value between 0 and 1. In Wageningen, The Netherlands, for instance, $V_{temp\ struc}$ equals 0.58 (weather data kindly provided by the Dept. of Meteorology and Air Quality, Wageningen University). Only in continental climates structurally showing one or more monthly temperatures below zero, may $V_{temp\ struc}$ exceed the value 1.

Figure 3.4 shows the response of the extrinsic variability of the intrinsically unstable ecosystem to the structured environmental variability. This graph was produced by computing the extrinsic stability of this system for a wide range of structured environmental fluctuations. The intrinsic yield variability is now given by the Y-intercept of these extrinsic variabilities, at which $V_{temp\ struc}$ equals zero. For this ecosystem, the intrinsic yield variability, $V_{yield\ int}$, equals 0.19.

When using field data instead of the simulation model output used here, the intrinsic yield variability (the intercept of the extrinsic yield variabilities) may be derived from extrapolation of the extrinsic stability of identical ecosystems, measured in a range of climates (*i.e.* under a range of structured environmental variability).

Figure 3.4 also shows that impact of the structured environmental variability on the extrinsic yield variability is non-linear. Small structured fluctuations show little impact on the extrinsic variability of the system. When subjected to a large structured environmental variability ($V_{temp\ struc}$ >

0.75), the intrinsic oscillations of the system are stabilised to some extent. Only when the structured variability exceeds 1, the oscillations may be fully neutralised, i.e. when months with temperatures below zero occur on a regular basis, during which herbage production of the simulated ecosystem is fully impeded.

*3.3.5 Ecosystem sensitivity*

Apart from the actual and extrinsic yield variability, the graphs in Figure 3.3 reveal some additional features of the two ecosystems involved. The shapes of the regression lines represent the sensitivity of the ecosystem to the stochastic environmental fluctuations. This sensitivity can be regarded as the inverse of the combined resistance (reluctance to change) and resilience (capacity to return to ecuilibrium) of the system. When an ecosystems is easily perturbed by stochastic temperature fluctuations (low resistance) and shows a slow recovery after this perturbation (low resilience), then its actual yield variability will show a sharp response to even small stochastic environmental fluctuations (high sensitivity), and hence a "steep" regression line in Figure 3.3.

A comparison of Figures 3.3a, b, and c shows that this sensitivity is dependent on the *structured* environmental variability. In other words: although the structured environmental fluctuations do not lead to temperature differences between years, they do have an effect on the actual variability of the yields. In the intrinsically stable system, stronger structured fluctuations lead to a progressively non-linear relationship. In a climate with no structured environmental variability (no seasonality: Figure 3.3a), the sensitivity is nearly equal for small and large stochastic environmental fluctuations, as the slope of the regression line is almost constant. In this climate, the actual yield variability will be low in decades with small stochastic temperature fluctuations, and high in decades with large fluctuations.

Contrastingly, in a climate with strong structured temperature fluctuations, the ecosystem shows a high sensitivity to small stochastic fluctuations (sharp increase on the left hand side of Figure 3.3c). However, only a small further increase of the actual yield variability is observed when the stochastic environmental fluctuations are progressively increased (flat slope on the right hand side of Figure 3.3c). Hence in these climates, the actual yield variability will be high for the majority of decades, in spite of the intrinsic stability of the ecosystem.

The sensitivity of the intrinsically unstable system shows an even more pronounced response to the environment (Figures 3.3d, e, and f). In absence of structured fluctuations, this ecosystem is largely unstable (Figure 3.3d). However, it is insensitive, or even slightly negatively sensitive to the extent of the stochastic environmental fluctuations. In fact, in this climate the ecosystem is "caught" in its own intrinsic cycle. It was shown in the previous paper (Chapter 2) that stochastic

environmental fluctuations may either magnify or compensate for this intrinsic cycle, depending on the timing of the individual temperature fluctuations in relation to the phase of the cycle. The slightly negative slope of the regression line indicates that *on average* the system is somewhat *stabilised* by stochastic temperature fluctuations in this climate.

When this unstable system is stabilised by structured temperature fluctuations, simultaneously its sensitivity is increased (Figures 3.3e and f). Under large structured environmental fluctuations (Figure 3.3e and f), the response of the system to the stochastic temperature variability progressively approaches the response of the intrinsically stable system (compare Figures 3.3c and e). It was shown in the previous paper (Chapter 2, Figures 2.19a,b) that in such a strongly seasonal climate, even the yield patterns over time may be nearly identical for an intrinsically stable and an intrinsically unstable system.

Finally note that in *all* climates, on average a lower actual yield variability is observed in the intrinsically unstable system than in the intrinsically stable system, during decades with a very high environmental variability (extreme right hand sides of the graphs in Figure 3.3). This paradox clearly underlines the complexity of analysis of yield stability in mixed pastures.

*3.3.6 Ecosystem predictability*

Finally, the predictability of the ecosystem is defined by the "goodness of fit" of the regression line, i.e. by the variance accounted for ($R^2$). The small predictability of the systems above is not the result of experimental noise, as the data points were produced by a mechanistic model (Chapter 2).

Instead part of it is caused by the timing of the individual stochastic fluctuations. During some decades the stochastic fluctuations may compensate for each other within each year, leading to small deviations of the annual average temperature (Figure 3.5a). In other decades, however, high and low stochastic fluctuations may occur in different years, respectively, leading to large deviations of the mean temperature between years (Figure 3.5b). As the mean amplitude of the stochastic fluctuations is identical in both graphs (i.e. 0.5), the growth and senescence rates of plant species may be assumed to be affected to more or less the same extent by each of temperature regimes. However, since the apparent stochastic environmental variability differs drastically, this leads to a "horizontal scattering" of the data points in Figure 3.3.

Additionally, the timing of the high and low stochastic environmental fluctuations in relation to possible intrinsic system oscillations is crucial. Figure 2.17 in the Chapter 2 illustrated that these stochastic fluctuations may either magnify or counteract these internal fluctuations, which either destabilises or stabilises the system, respectively. This leads to a "vertical scattering" of the data points in Figure 3.3.

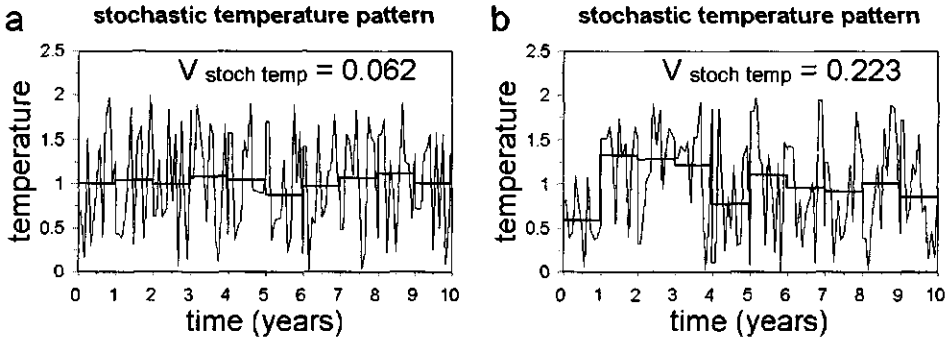


Figure 3.5: Two stochastic temperature patterns over a 10-year period. Single line: monthly mean temperature; bold line: annual mean temperature. The average temperature over 10 years equals 1 in both graphs, and the average amplitude of the fluctuations equals 0.5 in both graphs. Fluctuations compensate for each other within each year in graph a, leading to a stable annual mean temperature. In graph b high and low fluctuations occur in different years, leading to a high variability of the annual mean temperature.

Figures 3.3a, b, and c show that in an intrinsically stable ecosystem the predictability is declining (smaller $R^2$ ) under progressively increasing structured environmental fluctuations. Conversely, Figures 3.3 d, e, and f show the opposite response from an intrinsically unstable ecosystem. This, however, is the result of the very low sensitivity ("flat slopes") of the systems in graphs d and e, which leads to a small variance accounted for.

The small predictability of the intrinsically unstable systems may complicate the analysis of field data. In these analyses, a small $R^2$ may either show that an ecosystem is intrinsically unstable with a low predictability, or simply indicate that not all environmental variables are appropriately included.

## 3.4 Discussion

The previous paper (Chapter 2) extensively explored and conceptualised the complexity of the intrinsic properties and processes of grassland ecosystems, in particular of mixtures of perennial ryegrass and white clover. Additionally, the interactions of the modelled ecosystem with the effects of spatial scale, and environmental fluctuations were investigated. It was demonstrated how the extrinsic and the actual stability of modelled ecosystems can be computed from the intrinsic stability, by imposing structured and stochastic environmental fluctuations, respectively, on the ecosystem.

In the current paper a mathematical framework has been presented, which conversely enables the deduction of the extrinsic and intrinsic stability from the actual stability, as measured in

field experiments. This framework has been exemplified by using "field data", which were generated by the model of the previous paper (Chapter 2). The use of these "modelled field data" was preferred over the use of "experimental field data", in order to illustrate the mathematical framework with clear and significant responses of the ecosystem to the environment, and to eliminate experimental "noise".

It has been shown that the extrinsic ecosystem variability is defined by the extrapolated intercept of a regression between the actual yield variability and the stochastic environmental variability, as simultaneously observed during a large number of decades (Figure 3.3). Subsequently, the intrinsic stability may be deduced from the extrapolated intercept of a regression between the extrinsic yield variability and the structured environmental variability, as observed in a large number of climates (Figure 3.4).

Furthermore, complex interactions were established between the intrinsic ecosystem stability, the regime of structured environmental fluctuations (seasonality of the climate), and stochastic environmental fluctuations (e.g. daily, weekly, or monthly temperature deviations). It was predicted that in all climates, intrinsically stable mixed grasslands show stable yields or herbage masses during "quiet" decades, i.e. decades in which the average temperatures of all years were similar. Only during decades in which "warm" and "cold" years alternated, will the yields be destabilised (Figures 3.3a, b, c).

In contrast, the intrinsically unstable system showed largely fluctuating yields in temperate climates. However, the fluctuations were maximal during "quiet" decades. When the mean annual temperature fluctuated, yields of this ecosystem were on average slightly stabilised (Figure 3.3d). In continental climates, the stability and the responses to the environment of the intrinsically stable system approached those of an intrinsically stable ecosystem instead, with low yield fluctuations during very quiet decades, and stronger fluctuations when differences between the mean annual temperatures were larger (Figure 3.3f).

In short, in temperate climates, yield fluctuations of an intrinsically unstable ecosystem are the result of the intrinsic properties and processes. In continental climates they are caused by a combination of these properties and by the system's sensitivity to stochastic environmental fluctuations. The yield fluctuations of an intrinsically stable system are always the result of this sensitivity only.

Paradoxically, during decades with very large temperature differences between years, in all climates the yields of intrinsically unstable systems were on average slightly more stable than the yields of intrinsically stable systems (Figure 3.3). This paradox indeed challenges the desirability of intrinsically stable grassland systems in locations in which the environment shows large stochastic patterns. Additionally, it stresses that the yield fluctuations observed in experiments of a short

duration (e.g. five years), are hardly, if any, a reflection of the intrinsic properties and the management of the ecosystems studied in these experiments. In this paper, the simulation of two ecosystems during 200 *decades* in three climates was required to derive the extrinsic and the intrinsic stability levels from the "observed" yield patterns. Clearly, the use of long-term experiments is a prerequisite for the analysis of ecosystem stability.

It should be stressed that the high complexity of ecosystem behaviour, presented in this paper, was produced by a very simple simulation model (Chapter 2). Only two plant species (*Lolium perenne* and *Trifolium repens*) were simulated, which were managed under continuous grazing only. Most importantly, the ecosystems were confronted with the fluctuations of only one environmental variable, i.e. of the temperature. In contrast, "real" ecosystems may consist of a variety of plant species, showing extinctions and invasions, and may be subjected to complex and variable management regimes. Moreover, the environment of grasslands is defined by more variables than the temperature only. Therefore, drastically more complex dynamics may be expected from these real grassland ecosystems. In this light it is not surprising that a large variety of system dynamics of mixed swards has been reported in the literature.

Nonetheless, the mathematical framework presented in this paper may equally be applied to experimental field data, in order to deduct the extrinsic as well as the intrinsic stability of ecosystems from their actual stability patterns over time. The large quantities of yield data required for this deduction compels the use of long-term experiments, however. In the following chapter (Chapter 4), the framework will be applied to two of such long-term experiments, i.e. the Park Grass Experiment in the UK (Anonymous, 1991) and the Ossekampen in The Netherlands (Elberse *et al.*, 1983).

Rather than taking "snapshots" of ecosystem stability in short-term experiments, the application of the current framework to these long-term experiments provides an improved insight into the effects of grassland management on the intrinsic, the extrinsic and intrinsic stability, respectively. Therefore this framework enables the testing of model predictions against experimental data. Conversely, it can equally aid the identification of ecosystem properties and processes, which play an indispensable role in "real" ecosystems, yet which have not been incorporated into simulation models to date. Indeed the mathematical methodology presented in this paper may as a result bridge the gap between the theoretical ecological studies on the one hand, and the experimental agronomic studies on the other.

# Chapter 4: Identification of stable and unstable ecosystems in two long-term field experiments

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## Abstract

1) The analysis of the intrinsic properties and processes of ecosystems, which regulate the production stability of mixed grasslands, has been complicated by the environmental noise caused by stochastic weather fluctuations. As a result, ecosystem stability has been mostly studied using simulation models.

2) In this paper, the mathematical framework presented in Chapter 3, is applied to a number of experimental ecosystems in the Park Grass Experiment (UK) and at the Ossekampen (The Netherlands), which were subjected to various fertiliser and lime applications, and to a regime of either cutting or grazing, respectively. This framework enables to differentiate between the effects of ecosystem properties and the effects of environmental fluctuations on the stability of yields.

3) In the Park Grass Experiment, the yields of all plots studied appeared to be extrinsically unstable. Only small differences were found between various fertiliser treatments. However, for all fertiliser treatments, plots receiving lime showed a higher extrinsic stability than unlimed plots. The extrinsic stability of the plot receiving farmyard manure was lower than that of the plot receiving an equivalent of mineral nitrogen. Only part of this instability could be explained by the four-yearly applications of farmyard manure.

4) Also at the Ossekampen, only small differences arose between the extrinsic stability of plots receiving various fertiliser treatments. Instead, the grassland management of the plots had an overriding effect on these stability levels. Whereas the extrinsic stability of all cut plots was low, all grazed plots were nearly entirely stable.

5) It is argued that the nitrogen dynamics in grassland ecosystems have only a small impact on their extrinsic stability levels, in spite of the predictions by simulation models. Instead, pH-related soil processes and the grassland management play an overriding role in the maintenance of the production stability of mixed grassland.

6) It is conceivable that a large number of other processes, which regulate ecosystem stability, could be identified in other plots and experiments, using the same mathematical framework.

## 4.1 Introduction

Mixed grasslands, and especially mixtures of grass species and white clover (*Trifolium repens*), have frequently been associated with fluctuating, and hence unreliable yields. (Curll *et al.*, 1985a,b; Evans *et al.*, 1990; Orr *et al.*, 1990; Laws & Newton, 1992; Schwinning & Parsons, 1996a,b; Fothergill *et al.*, 2000). The effects of single management factors on short-term clover performance (<5 yrs) have been well studied (e.g. Curll *et al.*, 1985a,b; Grant *et al.*, 1985; Evans *et al.*, 1990; Frame, 1990; Orr *et al.*, 1990; Parsons *et al.*, 1991a; Barthram *et al.*, 1992; Evans *et al.*, 1992; Gilliland, 1996; Nassiri, 1998). However, the identification of the processes and interactions which underlie the fluctuating yields of mixed grasslands, has been complicated by the variable environment in field experiments. The segregation of the effects of internal ecosystem processes and the effects of environmental fluctuations on the stability of yields has been a challenge to date. Some interesting conclusions were drawn indirectly from the yield fluctuations in the Park Grass Experiment, which confirmed the destabilising effects of competition for light (Silvertown & Dodd, 1994), and the stabilising effects of competition for nutrients (Silvertown, 1980), as predicted by the simulation model in Chapter 2.

The stabilising or destabilising nature of intrinsic ecosystem processes has been mostly studied in theoretical ecological studies, using simulated grassland systems in a mostly constant environment (e.g. Noy-Meir, 1975; Parsons *et al.* 1991b; Parsons *et al.*, 1994; Thornley *et al.*, 1995; Schwinning & Parsons 1996a, b). However, it has been argued in the previous chapters (Chapters 2 and 3), that the temporal yield patterns of grassland ecosystems which are predicted by these models, may differ largely from those observed in field experiments, as these models do not only omit the direct effects of the environment on yield variability, but also the more complex interactions between the intrinsic ecosystem processes and the environmental variability.

In an attempt to bridge the gap between the results of experimental studies and theoretical studies, a conceptual framework was presented in the Chapter 2, which defined three concepts of stability. First the *actual* stability was defined as the stability of yields in a "real" environment, in which fluctuations of environmental variables (e.g. rainfall, temperature) consist of seasonal (structured) components and stochastic components. As the environmental variability may vary over time, the actual stability level of an ecosystem is limited to the location and to the time-course during which it has been observed: a different level may be expected when the same system is observed on either a different location, or during a subsequent observation period.

Contrastingly, the stability of an ecosystem in a hypothetical, constant environment, such as that applied in most simulation models, was defined as the *intrinsic* stability level. This intrinsic

stability level is dependent on internal ecosystem properties only. Therefore, it is independent of environmental fluctuations, and will remain constant over time and between locations.

Finally, the *extrinsic* stability of an ecosystem was defined as the stability in a climate which shows seasonal (i.e. structured) fluctuations, yet no stochastic environmental fluctuations. Ignoring possible climate changes, the seasonal environmental fluctuations are by definition identical between years. Therefore, the extrinsic stability level will remain constant over time. However, it does depend on the climate, and hence the location of the ecosystem.

It was consequently argued that the extrinsic stability is a more reliable indicator of system stability than the actual stability, as it does not depend on the coincidental weather conditions during the observation period. At the same time, as the extrinsic stability does depend on the more complex effects of the climate on the variability of yields, the extrinsic stability is a more genuine reflection of the stability of yields, experienced in the field, than the intrinsic stability.

In Chapter 3, it was explained that in theoretical studies, the extrinsic and actual stability levels of ecosystems can be derived relatively easily, i.e. by imposing structured and stochastic environmental fluctuations on the modelled ecosystems, respectively. Additionally, a mathematical framework was presented, with which the actual, extrinsic and intrinsic stability levels can be derived from field experiments, instead. It was argued that this framework enables the testing of the predictions by simulation models against field data, as well as the identification from these field data of essential factors regulating stability, that have not been incorporated into simulation models to date.

In this chapter, the mathematical framework is applied to the yield data of two long-term experiments. First the stability is studied of a number of experimental plots of the Park Grass Experiment (Rothamsted Experimental Station, UK), which differ in fertiliser and liming treatment. Secondly, plots of the Ossekampen Experiment (Plant Research International, The Netherlands) are studied, which differ in fertiliser treatment, and grassland management regime.

## 4.2 The Park Grass Experiment

### *4.2.1 Materials and Methods*

**Experimental lay-out and treatments**

The Park Grass Experiment is the oldest existing long-term grassland experiment, as it was initiated in 1856 and has been run continuously to date. It involves a large number of plots with

Table 4.1: Fertiliser and lime treatments of the Park Grass Experiment plots selected for analysis (Anonymous, 1991).

| Plot number | Acronym used in this paper | N application ammonium sulphate) (kg $ha^{-1}$ $yr^{-1}$) | P application (kg $ha^{-1}$ $yr^{-1}$) | K application (kg $ha^{-1}$ $yr^{-1}$) | Limed | Other nutrients |
|---|---|---|---|---|---|---|
| 3U-3d | control unlimed | - | - | - | no | - |
| 3L-3a | control limed | - | - | - | yes | - |
| 1U-1d | N unlimed | 96 | - | - | no | - |
| 1L-1a | N limed | 96 | - | - | yes | - |
| 7U-7d | PK unlimed | - | 35 | 225 | no | Mg |
| 7L-7a | PK limed | - | 35 | 225 | yes | Mg |
| 9U-9d | NPK unlimed | 96 | 35 | 225 | no | Mg |
| 9L-9a | NPK limed | 96 | 35 | 225 | yes | Mg |

different fertiliser treatments, which are all cut for conservation twice yearly. For full details on treatments and plot lay-out see Anonymous (1991) and Warren & Johnston (1963). Three times in its life span has the experiment been changed: first in 1903, when all existing plots were split into halves. From that moment, one half received lime every four years, whereas the other half remained unchanged. In 1965, each fertiliser treatment was split into four quarters, three of which were limed to maintain soil pH levels of 5, 6, and 7 respectively, the fourth quarter receiving no lime. Until 1960, dry matter production was measured by the amount of hay made from each plot. From 1960 onwards fresh herbage was cut at the hay-making stage, using a flail harvester.

In Chapter 2, the importance of the soil nitrogen status on the production stability of mixed grasslands was stressed, and the importance of the soil mineralisation processes was hypothesised. Therefore the following fertiliser treatments were selected for analysis: no fertiliser (control), nitrogen only, nitrogen with phosphorus and potassium (all major nutrients) and phosphorus with potassium only (nitrogen is the limiting factor). Within each fertiliser treatment the unlimed quarter was chosen, and the quarter which has received lime applications since 1903 and has been maintained at a soil pH 7 since 1965. Details of each treatment are summarised in Table 4.1.

**Data analysis**

Within each year, first and second cut yields were summed for each plot to obtain annual plot yields. In Chapters 2 and 3, the actual yield stability was related to stochastic temperature fluctuations only, which were produced by the simulation model. However, it was also shown that

in temperate climates the temperature pattern generally shows a large structured component, and only a small stochastic component. Conversely, rainfall shows a more stochastic pattern over time, leading to larger between-year variations. Therefore the actual variability of rainfall during each decade is included here to explain the actual yield variability within each decade. Monthly rainfall data were summed from October to September the following year, to obtain the total precipitation during the growing season of each grass crop. Temperature data were also summed for the months October to September.

Rainfall and temperature data were incomplete until 1915. Furthermore, the change in harvesting methodology in 1960 and the new liming scheme in 1965 may be expected to have increased the variability of yields at least temporarily, until a new ecuilibrium (Chapter 2) had been reached (Chapter 3). Therefore, data were disregarded between 1960, when the harvesting methodology was changed, and 1975, ten years after the liming scheme was altered. As a result only four full decades between 1915 and 1959, and two full decades between 1975 and 1999 could be taken into account. In Chapter 3 it was shown that more than six data points are required to provide significant relationships between the actual yield variability and the stochastic environmental variability, due to the low "predictability" of some ecosystems. For this reason, each *progressive* decade was taken into account in the current study, e.g. 1915-1924, 1916-1925, 1917-1926. This resulted in 52 actual variability values for each plot. Note that successive "decades" have 9 years in common, and can therefore no longer be considered to be independent. Nonetheless, the use of progressive decades is required as other suitable grassland experiments older than 60 years do not exist.

The change of the harvesting method in 1960 caused *different* yield levels before and after this date. However, the actual yield variability, as defined in Chapter 3, is independent of the yield *level*, as it scales the yield fluctuations to the average yield. Therefore the actual yield variability of decades before and after 1960 were treated identically.

The actual yield variability of each plot, as well as the stochastic temperature variability and the stochastic rainfall variability, were all computed for each progressive decade, according to the mathematical framework presented in Chapter 3. Multiple linear regressions were performed to explain the actual yield variability by the stochastic variability of both precipitation and temperature. In cases where either of the explaining variables did not have a slope significantly different from zero, single linear regressions were performed, explaining the actual yield variability with *either* the stochastic precipitation variability or the stochastic temperature variability.

Table 4.2: Results of multiple and single linear regressions of the actual yield variability of eight plots of the Park Grass Experiment explained by the stochastic precipitation and temperature variability. Asterisks indicate significance level at which the intercept and the slopes are different from zero: *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$. Fully significant regressions, with all slope(s) significantly different from 0 ($p < 0.05$) are indicated in bold.

| Treatment | Independent variables | Extrinsic variability (intercept) | Sensitivity (slope) | Predictability ($R^2$) | p |
|---|---|---|---|---|---|
| Control limed | $V_{stoch\ rain}$ | 0.29 *** | 0.95 *** | 0.31 | < 0.001 |
| | $V_{stoch\ temp}$ | | -1.30 | | |
| | **$V_{stoch\ rain}$** | **0.23 *** ** | **0.90 *** ** | **0.28** | **< 0.001** |
| Control unlimed | $V_{stoch\ rain}$ | 0.48 *** | -0.32 | 0.03 | n.s. |
| | $V_{stoch\ temp}$ | | 0.08 | | |
| | $V_{stoch\ rain}$ | 0.49 *** | -0.32 | 0.03 | n.s. |
| | $V_{stoch\ temp}$ | 0.44 *** | -0.15 | 0.00 | n.s. |
| N limed | $V_{stoch\ rain}$ | 0.32 *** | 0.22 | 0.07 | n.s. |
| | $V_{stoch\ temp}$ | | -1.09 | | |
| | $V_{stoch\ rain}$ | 0.27 | 0.18 | 0.02 | n.s. |
| | $V_{stoch\ temp}$ | 0.36 | -0.94 | 0.04 | n.s. |
| N unlimed | **$V_{stoch\ rain}$** | **0.82 *** ** | **-0.67 *** | **0.25** | **< 0.001** |
| | **$V_{stoch\ temp}$** | | **-3.24 **** | | |
| PK limed | $V_{stoch\ rain}$ | 0.16 *** | 0.49 ** | 0.19 | < 0.01 |
| | $V_{stoch\ temp}$ | | -0.18 | | |
| | **$V_{stoch\ rain}$** | **0.15 *** ** | **0.48 **** | **0.19** | **< 0.01** |
| PK unlimed | $V_{stoch\ rain}$ | 0.44 *** | -0.79 *** | 0.23 | < 0.01 |
| | $V_{stoch\ temp}$ | | 0.24 | | |
| | **$V_{stoch\ rain}$** | **0.45 *** ** | **-0.78 *** ** | **0.23** | **< 0.001** |
| NPK limed | **$V_{stoch\ rain}$** | **0.23 *** ** | **0.84 *** ** | **0.46** | **< 0.001** |
| | **$V_{stoch\ temp}$** | | **-3.73 *** ** | | |
| NPK unlimed | **$V_{stoch\ rain}$** | **0.34 *** ** | **1.47 *** ** | **0.63** | **< 0.001** |
| | **$V_{stoch\ temp}$** | | **-6.06 *** ** | | |

Finally, in Chapter 3 the extrinsic yield variability was quantified as the intercept of the regressions, when the stochastic variability of both rainfall and temperature equal zero. The sensitivity of the ecosystem to the stochastic environmental variability was defined by the slopes of the regression, and the system's predictability was defined by the variance accounted for by the multiple regression.

*4.2.2 Results*

A summary of the regression statistics is given in Table 4.2. The actual yield variabilities of the unlimed N plot, and of both the limed and the unlimed NPK plot showed significant responses to both the stochastic rainfall and temperature variability. The limed control plot and both the limed and the unlimed PK plots responded only to the stochastic rain variability. The actual yield variability of the unlimed control and of the limed N plot could not be explained by either of the two independent variables.

Figure 4.1 illustrates the impact of the stochastic rainfall variability and the stochastic temperature variability on the actual yield variability of the Park Grass Experiment plots. Best linear fits are shown by the planes. Zero slopes of the planes indicate sensitivities which are not significantly different from zero. "Peaks" and "valleys" in these planes indicate data points with large deviations from these fits. The remaining data points are located on the surfaces of the planes. These three-dimensional graphs allow the prediction of the actual yield variability under a wide range of conceivable environments, e.g. an environment with no stochastic rainfall variability (left wall of graphs), an environment with no stochastic temperatures fluctuations (back wall of graphs), or a structured environment with neither stochastic rainfall nor temperature fluctuations (y-axis in the "back corner" of the graph).

Most strikingly, all plots which received lime show lower extrinsic variabilities (y-intercepts) than the unlimed plots. However, all intercepts are significantly larger than zero, indicating that none of the plots are intrinsically stable. Two of the limed plots, i.e. the control and the PK plot show positive or insignificant sensitivities (Chapter 3) to stochastic rainfall fluctuations, and insignificant sensitivities to stochastic temperature fluctuations. The limed NPK plot also shows a positive sensitivity to the rainfall variability, but a significantly negative sensitivity to the temperature fluctuations. The limed and unlimed NPK plots are the only ecosystems which have at least a limited "environmental window", in which the yields would be stable, i.e. in environments with low stochastic rain variability, combined with high stochastic temperature variability.

This evidence suggests that the limed plots are intrinsically unstable, yet stabilised to some extent by structured rainfall and temperature fluctuations (compare with Figures 3.3e,f in Chapter 3). Alternatively, it is conceivable that these plots are in fact intrinsically stable, but show a non-linear response to the stochastic fluctuations (see Figures 3.3a, b, c in Chapter 3). Note that most data points are concentrated in the "front corner" of the graphs, as decades with a small stochastic rainfall variability rainfall as well as a small temperature variability are rare. The absence of data near the y-axis makes the extrapolation of the actual variability a hazardous undertaking (see also the graphs in Figures 3.3 in Chapter 3).

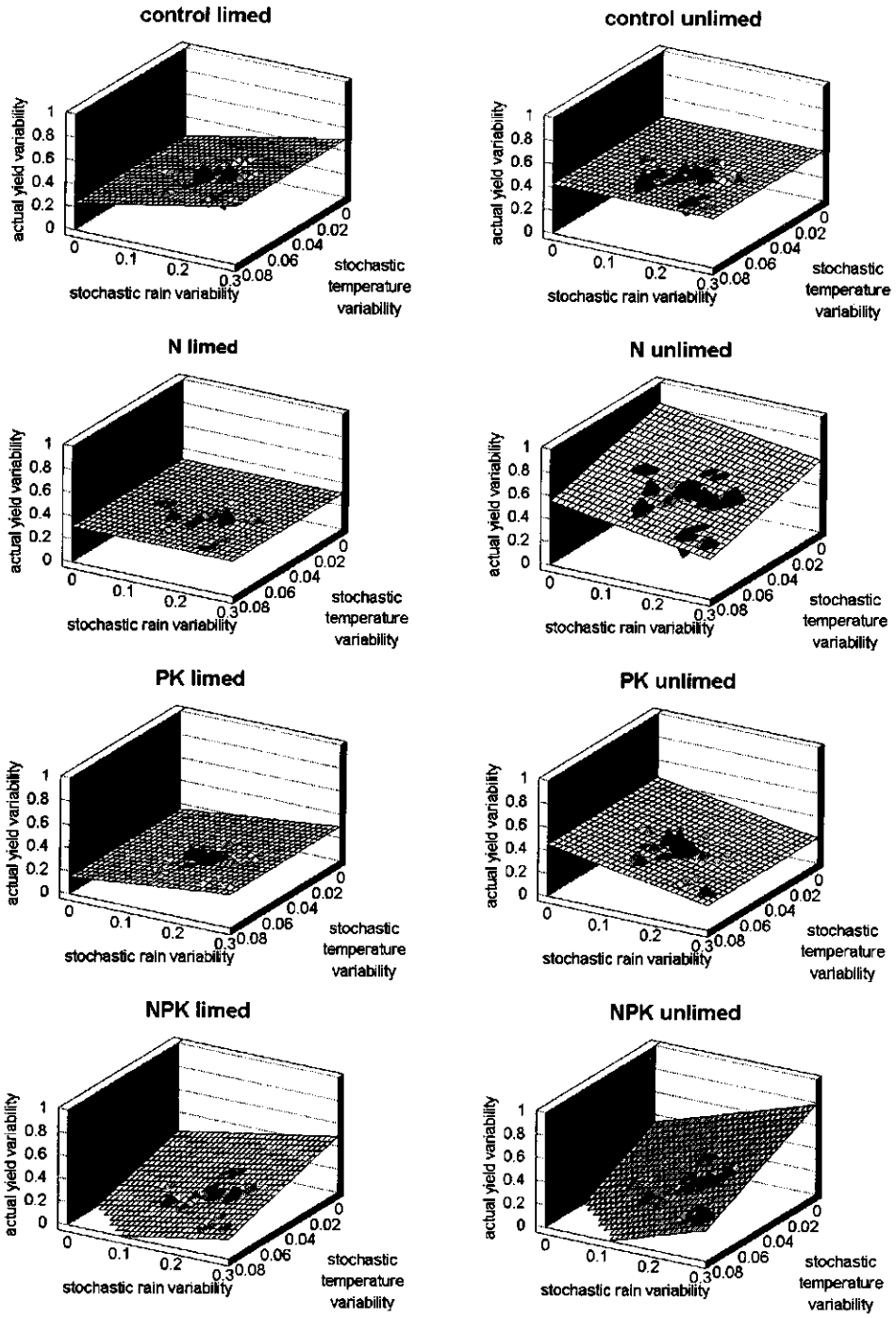


Figure 4.1: Actual yield variability of PGE plots against the stochastic rainfall and temperature variability. Planes indicate best linear fits. Insignificant relations are shown by zero slopes. Data with large deviations are indicated by "peaks" and "valleys".

Contrastingly, the unlimed control, the unlimed N and the unlimed PK plot show large extrinsic variabilities (intercept > 0.4) and negative or insignificant sensitivities to both environmental variables, indicating that these plots are intrinsically unstable, and hardly stabilised by structured environmental fluctuations (compare with Figure 3.3d in Chapter 3).

## 4.3 A special case: farmyard manure vs. fertiliser applications

In addition to the impact of the nitrogen dynamics on the stability of grass-clover ecosystems, the importance of spatial disturbances of grasslands was conceptually explored in Chapter 2. It was shown that local disturbances at a patch-scale leading to spatial heterogeneity, could stabilise intrinsically oscillating ecosystems, whereas these systems could be further destabilised by uniform disturbances at a field-scale. It was consequently hypothesised that applications of farmyard manure (FYM) would stabilise intrinsically oscillating systems, presuming that the FYM dressings would lead to spatial heterogeneity. It was also argued that fertiliser applications would instead lead to spatial homogeneity, and therefore have a negative effect on system stability. To investigate the effects of the scale of disturbances, two additional plots of the Park Grass Experiment were selected for analysis. These were plots 19-19/2 ("FYM treatment") and 16L-16b ("fertiliser treatment").

### *4.3.1 Materials and Methods*

Plot 19-19/2 had received 35 tonnes $ha^{-1}$ of FYM of bullocks, as well as approximately 3150 kg of lime (CaO) $ha^{-1}$, every fourth year since 1905 (except FYM in 1917). On average each FYM application supplied the equivalent of 240 kg nitrogen, which equals 60 kg nitrogen $ha^{-1}$ $year^{-1}$ (P.R. Poulton, *pers. comm.*). Lime applications on this plot were only commenced in 1920, and therefore only the herbage yields from 1930 were taken into account.

The fertiliser treatment of plot 16L-16b was similar to the treatment of plot 9L-9a ("limed NPK", section 4.2.1), except for the nitrogen dressings, which equalled 48 kg $ha^{-1}$ $year^{-1}$, and which were applied in the form of sodium nitrate.

The data analysis of the "FYM" and the "fertiliser" plot was identical to the analysis of the plots in section 4.2.1.

### *4.3.2 Results*

Table 4.3 presents the results of the multiple linear regressions of the actual yield variability of the FYM and the fertiliser plot, with the stochastic rain and temperature variability as independent variables. These results are illustrated in Figure 4.2.

Table 4.3: Results of multiple and single linear regressions of the actual yield variability of the "fertiliser" and the "FYM" plots of the Park Grass Experiment explained by the stochastic precipitation and temperature variability. Asterisks indicate significance level at which the intercept and the slopes are different from zero: *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$. Fully significant regressions, with all slope(s) significantly different from 0 ($p < 0.05$) are indicated in bold.

| Treatment | Independent variables | Extrinsic variability (intercept) | Sensitivity (slope) | Predictability ($R^2$) | p |
|---|---|---|---|---|---|
| Fertiliser | $V_{stoch\ rain}$ | 0.10 *** | 0.69 *** | 0.52 | < 0.001 |
| | $V_{stoch\ temp}$ | | -0.47 | | |
| | **$V_{stoch\ rain}$** | **0.07 *** ** | **0.67 *** ** | **0.50** | **< 0.001** |
| FYM | $V_{stoch\ rain}$ | 0.25 *** | 0.36 | 0.12 | n.s. |
| | $V_{stoch\ temp}$ | | -0.07 | | |
| | **$V_{stoch\ rain}$** | **0.24 *** ** | **0.36 *** | **0.12** | **< 0.05** |
| | $V_{stoch\ temp}$ | 0.32 *** | -0.43 | 0.01 | n.s. |

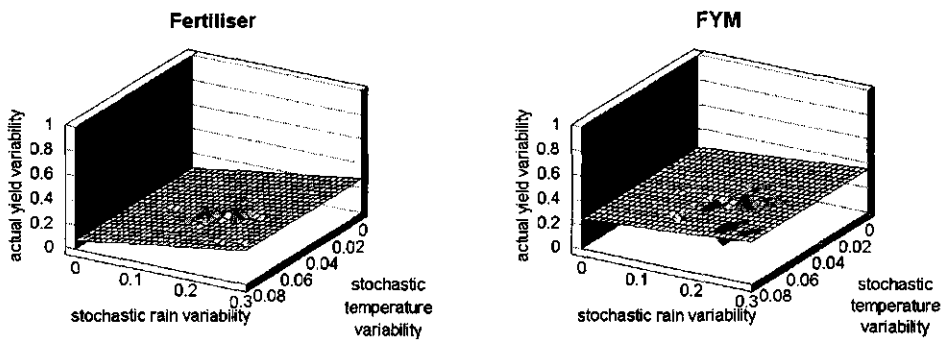


Figure 4.2: Actual yield variability of the "fertiliser" and "FYM" plots of the PGE against the stochastic rainfall and temperature variability. Planes indicate best linear fits. Insignificant relations are shown by zero slopes. Data with large deviations are indicated by "peaks" and "valleys".

Table 4.3 and Figure 4.2 show that both plots responded significantly to the stochastic rainfall variability only. The fertilised plot had a lower extrinsic yield variability (Y-axis), and a stronger sensitivity (slope) to the stochastic rainfall variability than the FYM plot. Therefore, the fertilised plot had a higher extrinsic stability.

*4.3.3 Correction for four-yearly applications of FYM*

It is conceivable that the difference between the yield fluctuations of the fertilised plot and the FYM plot were partly caused by the fact that the fertilised plot received constant quantities of nutrients each year, whereas nutrients were supplied to the FYM plot only every fourth year. Therefore the yields of the FYM plot were plotted against the number of years since the last FYM

application (Figure 4.3). Note that due to the change of the harvesting method in 1960, the yield level (as opposed to the actual yield variability) before and after this date are different, and are therefore treated separately.

Figure 4.3 shows that before 1960, yields showed no significant correlation with the number of years elapsed since the last FYM manure application. However, after 1960, yields show a weak but significant negative correlation ($R^2 = 0.21$, $p < 0.05$) with the number of years since the last dressing. This correlation was absent for the fertilised plot, and is therefore unlikely to be the result of coincidental 4-yearly cycles of the environment.

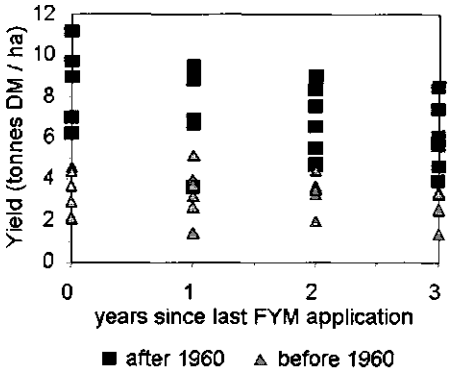


Figure 4.3: The relation between yields of the FYM plot in the PGE, and the time elapsed since the last FYM application.

In order to separate the effects of the 4-yearly dressings from the effects of FYM applications *per se* on the system stability, the yields of the FYM plot after 1960 were corrected for this 4-yearly cycle, using Owen & Jones (1990) (their Chapter 7: "deseasonalisation"). A multiple linear regression was again performed, explaining the actual variability of these corrected yields by the stochastic rainfall and temperature variability (Table 4.4).

Table 4.4 and Figure 4.4 show that the variability of the corrected yields of the FYM plots showed a slightly lower extrinsic variability and a more positive sensitivity to the stochastic rainfall variability than the variability of the uncorrected yields (compare with Table 4.3 and Figure 4.2). This indicates that at least part of the yield fluctuations on the plot receiving FYM, were caused by

Table 4.4: Results of multiple and single linear regressions of the actual variability of the yields of the "FYM" plot in the PGE, corrected for the variability caused by the 4-yearly FYM applications, and explained by the stochastic precipitation and temperature variability. Asterisks indicate significance level at which the intercept and the slopes are different from zero: *: $p<0.05$. **: $p<0.01$, ***: $p<0.001$. Fully significant regressions, with all slope(s) significantly different from 0 ($p < 0.05$) are indicated in bold.

| Treatment | Independent variables | Extrinsic variability (intercept) | Sensitivity (slope) | Predictability ($R^2$) | p |
|---|---|---|---|---|---|
| FYM (corrected) | $V_{stoch\ rain}$ | 0.21 ** | 0.51 | 0.21 | < 0.05 |
| | $V_{stoch\ temp}$ | | 0.00 | | |
| | **$V_{stoch\ rain}$** | **0.21 *** ** | **0.51 **** | **0.21** | **< 0.01** |
| | $V_{stoch\ temp}$ | 0.33 *** | -0.61 | 0.01 | n.s. |

the four-yearly nutrient applications, as opposed to the fertilised plot, which received annual dressings of nutrients. Nevertheless, even when corrected for this discrepancy, the FYM plot showed a larger extrinsic variability than the fertilised plot. As a result, the fertilised ecosystem was more stable than the system receiving FYM, in spite of the assumed larger spatial heterogeneity of the latter.

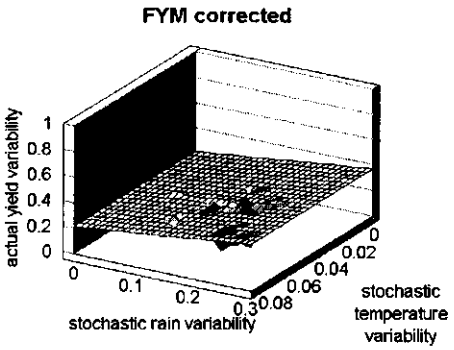


Figure 4.4: Actual variability of the yields of the "FYM" plot in the PGE, corrected for the variability caused by the four-yearly FYM applications, and explained by the stochastic rainfall and temperature variability. Plane indicates best linear fit. Insignificant relations are shown by zero slopes. Data with large deviations are indicated by "peaks" and "valleys".

## 4.4 The Ossekampen Experiments

### *4.4.1 Materials and Methods*

**Experimental lay-out and treatments**

The Ossekampen experiments are located on a river clay soil near Wageningen, The Netherlands. Two experiments were conducted since 1958: 1) a cutting experiment, in which plots receiving various combinations of fertiliser were cut twice yearly, and 2) a grazing experiment, in which plots receiving the same fertiliser combinations were grazed rotationally with cattle. On these grazed plots, yields were measured three times a year under cages, which were moved annually.

The fertiliser treatments in the cutting experiment were laid out in 2 replications. The treatments selected for the current study were: the unlimed control plot, the limed control plot, the

Table 4.5: Fertiliser treatments, lime treatments and management of the Ossekampen plots selected for analysis.

| treatment | # plots | start | N application (kg $ha^{-1}$ $yr^{-1}$) | P application (kg $ha^{-1}$ $yr^{-1}$) | K application (kg $ha^{-1}$ $yr^{-1}$) | limed |
|---|---|---|---|---|---|---|
| cut unlimed control | 2 | 1958 | 0 | 0 | 0 | no |
| cut limed control | 2 | 1958 | 0 | 0 | 0 | yes |
| cut N | 2 | 1966 | 160 | 0 | 0 | no |
| cut PK | 2 | 1958 | 0 | 25 | 175 | no |
| cut NPK | 2 | 1958 | 160 | 35 | 300 | no |
| grazed unlimed control | 2 | 1958 | 0 | 0 | 0 | no |
| grazed limed control | 1 | 1958 | 0 | 0 | 0 | yes |
| grazed PK | 1 | 1958 | 0 | 17 | 50 | no |
| grazed NPK | 2 | 1958 | 60 | 17 | 50 | no |

unlimed nitrogen plot, the unlimed PK plot, and the unlimed NPK plot. The unlimed nitrogen treatment was only commenced in 1966. In the grazing experiment, only the unlimed control and the unlimed NPK were laid out in duplicate. The limed control and the unlimed PK plots, which were also selected, had no replications. Details of the treatments in both experiments are given in Table 4.5. For more information on the experiment, see Elberse *et al.* (1983).

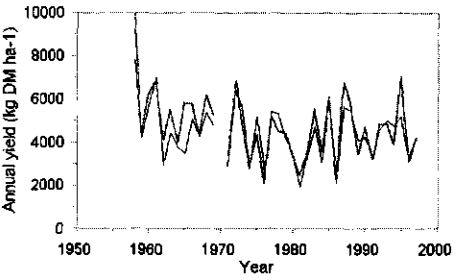


Figure 4.5: Annual yields of the duplicated unlimed control plots of the cutting experiment of the Ossekampen from 1958 until 1997.

**Data analysis**

Yield and environmental data were dealt with in a manner identical to those of the Park Grass Experiment. The first decade of the experiment was disregarded to allow the ecosystems to reach their ecuilibria, as the declining yields at the start of experiment (see Figure 4.5) would lead to high actual yield variabilities, which would be related to the changing fertiliser regime, rather than to the stability properties of the plots (Chapter 3). The data from 1969 until 1997 resulted in 20 progressive decades. In the replicated plots, yield patterns over time were nearly identical between duplications ($R^2 = 0.88$) in spite of the fluctuating yields between years (Figure 4.5). Therefore, data of replications were pooled within treatments, resulting in 40 observations per treatment.

Table 4.6: Results of multiple linear regressions of the actual yield variability of the five cut plots of the Ossekampen cutting experiment, explained by the stochastic precipitation and temperature variability. Asterisks indicate significance level at which the intercept and the slopes are different from zero: *: $p<0.05$. **: $p<0.01$, ***: $p<0.001$.

| Treatment | Independent variables | Extrinsic variability | Sensitivity (slope) | Predictability ($R^2$) | p |
|---|---|---|---|---|---|
| Cut control unlimed | $V_{stoch\ rain}$ | 0.54 *** | -0.73 *** | 0.44 | < 0.001 |
| | $V_{stoch\ temp}$ | | -2.27 *** | | |
| Cut control limed | $V_{stoch\ rain}$ | 0.56 *** | -0.55 ** | 0.59 | < 0.001 |
| | $V_{stoch\ temp}$ | | -3.84 *** | | |
| Cut N unlimed | $V_{stoch\ rain}$ | 0.55 *** | -0.38 ** | 0.49 | < 0.001 |
| | $V_{stoch\ temp}$ | | -1.85 ** | | |
| Cut PK unlimed | $V_{stoch\ rain}$ | 0.68 *** | -0.66 ** | 0.64 | < 0.001 |
| | $V_{stoch\ temp}$ | | -5.09 *** | | |
| Cut NPK unlimed | $V_{stoch\ rain}$ | 0.49 *** | -0.49 * | 0.40 | < 0.001 |
| | $V_{stoch\ temp}$ | | -3.09 *** | | |

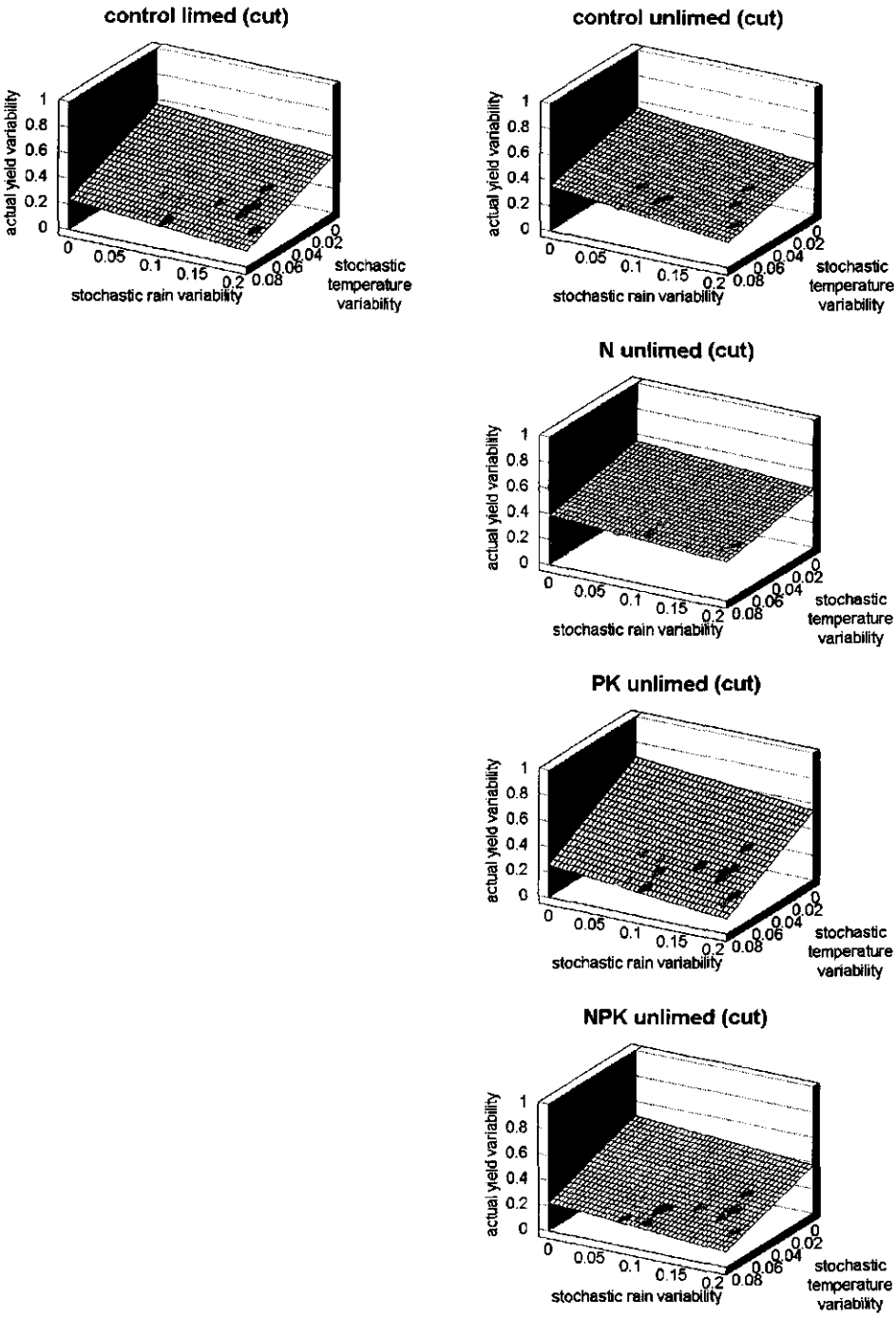


Figure 4.6: Actual yield variability of cut plots at the Ossekampen, against the stochastic rainfall and temperature variability. Planes indicate best linear fits. All relations are significant. Data with large deviations are indicated by "peaks" and "valleys".

*4.4.2 Results (cutting experiment)*

For the cutting experiment, the results of the multiple linear regressions of the actual yield variability against the stochastic rainfall and temperature variability are given in Table 4.6. For all plots the actual yield variability was significantly related to both the stochastic rainfall and temperature variability. All treatments showed similar responses to the stochastic rainfall and temperature fluctuations: all plots showed a large extrinsic variability and a negative sensitivity to both rainfall and temperature variability. Figure 4.6 illustrates these responses. Again, the planes indicate best linear fits, while data with large deviations from these planes are given by "peaks" and "valleys". These results indicate that all cut ecosystems at the Ossekampen experiment are intrinsically unstable, and not stabilised by structured environmental fluctuations (compare with Figure 3.3d in Chapter 3). The predictability of all systems is higher than the predictability of the plots at the Park Grass Experiment.

The NPK plots showed the smallest extrinsic variability. During the 40 years of the experiment these plots had developed from a mixture of grasses and legumes (legume cover of 48% in 1958) into a grass monoculture (legume cover of 1% in 1997). However, this ecosystem's extrinsic variability was still significantly larger than zero, and therefore the ecosystem was not entirely stable.

The limed control plot showed an extrinsic variability similar to the unlimed control plot, despite the differences between the pH between the treatments in 1997 (pH = 6.25 and 3.75 for the limed and unlimed control, respectively). However, the limed control plots showed a stronger

Table 4.7: Results of multiple linear regressions of the actual yield variability of the four grazed plots of the Ossekampen grazing experiment, explained by the stochastic precipitation and temperature variability. Asterisks indicate significance level at which the intercept and the slopes are different from zero: *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$. Fully significant regressions, with all slope(s) significantly different from 0 ($p < 0.05$) are indicated in bold.

| Treatment | Independent variables | Extrinsic variability | Sensitivity (slope) | Predictability ($R^2$) | p |
|---|---|---|---|---|---|
| Grazed control unlimed | $V_{stoch\ rain}$ | 0.27 *** | 0.22 | 0.36 | < 0.001 |
| | $V_{stoch\ temp}$ | | -1.76 ** | | |
| | **$V_{stoch\ temp}$** | **0.32 *** ** | **-2.15 *** ** | **0.33** | **< 0.001** |
| Grazed control limed | **$V_{stoch\ rain}$** | **0.25 *** ** | **0.44 *** | **0.78** | **< 0.001** |
| | **$V_{stoch\ temp}$** | | **-2.50 *** ** | | |
| Grazed PK unlimed | $V_{stoch\ rain}$ | 0.01 | 0.92 *** | 0.88 | < 0.001 |
| | $V_{stoch\ temp}$ | | -0.13 | | |
| | **$V_{stoch\ rain}$** | **0.003** | **0.94 *** ** | **0.88** | **< 0.001** |
| Grazed NPK unlimed | **$V_{stoch\ rain}$** | **0.15 *** ** | **0.44 *** ** | **0.74** | **< 0.001** |
| | **$V_{stoch\ temp}$** | | **-1.19 *** ** | | |

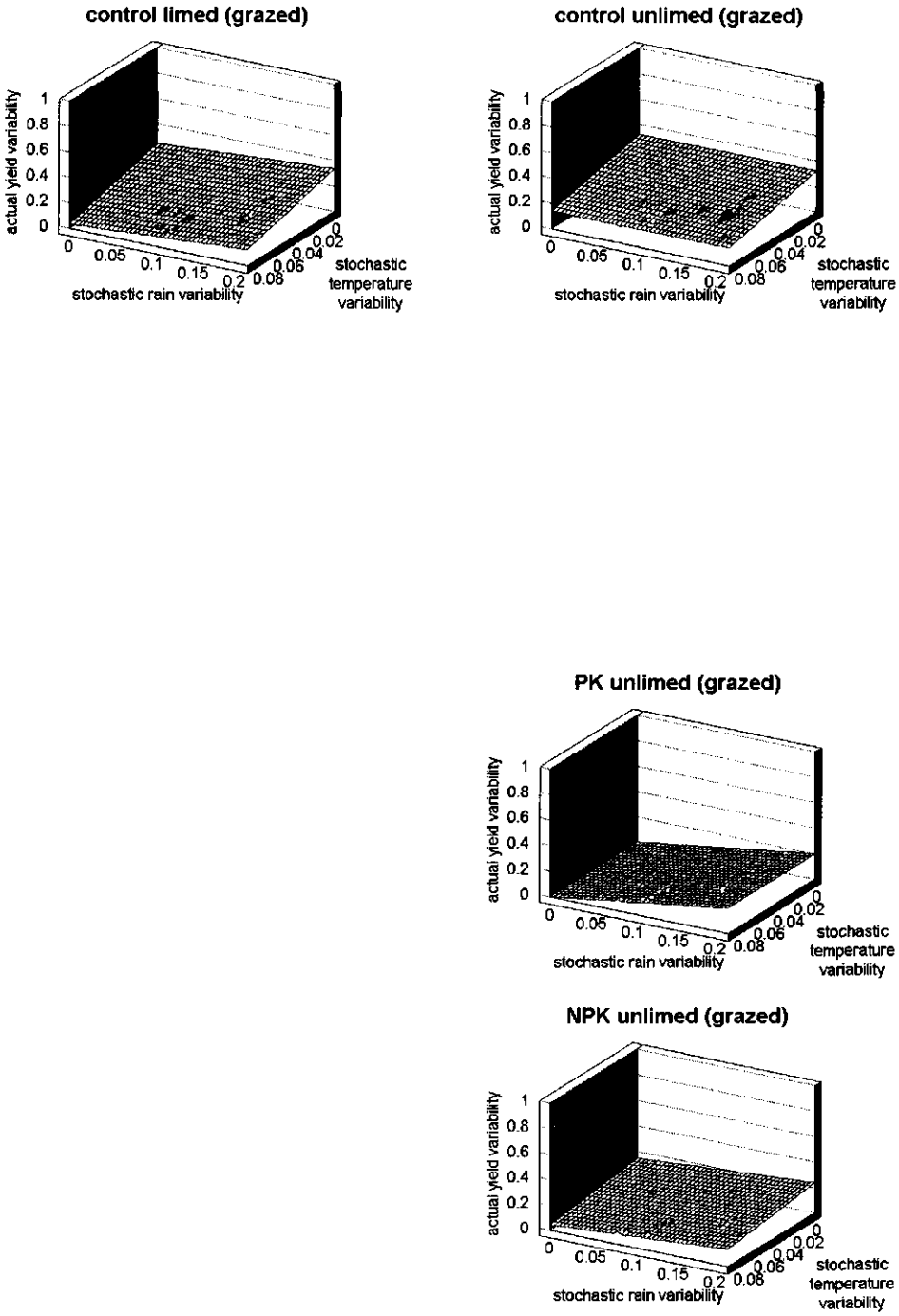


Figure 4.7: Actual yield variability of grazed Ossekampen, plotted against the stochastic rainfall and temperature variability. Planes indicate best linear fits. Insignificant relations are given by zero slopes. Data with large deviations are indicated by "peaks" and "valleys".

negative sensitivity to the stochastic temperature variability, resulting in a lower actual yield variability.

*4.4.3 Results (grazing experiment)*

Table 4.7 presents the results of the multiple and single linear regressions of the grazing experiment at the same site. In the grazing experiment, the limed control plot and the NPK plot showed significant multiple regressions, with high predictabilities (Chapter 3). Multiple regressions on the unlimed control plot and the PK plot were significant, but the slopes of the stochastic rainfall variability and of the stochastic temperature variability were not significantly different from zero, respectively. However, the unlimed control plot was significant related to the stochastic temperature fluctuations, whereas the PK plot was significantly related to the rainfall variability.

Figure 4.7 illustrates the response of the actual yield variability of the grazed plots to the environmental fluctuations. All plots show qualitatively similar responses, which clearly differ from the responses shown by the cut plots (compare with Figure 4.6). Most strikingly, the extrinsic variability of each of the grazed plots is much lower than its cut counterpart, indicating a larger extrinsic stability. Secondly, each plot shows a positive or insignificant sensitivity to stochastic rainfall fluctuations, and only a small negative sensitivity to stochastic temperature fluctuations. This means that these ecosystems are almost extrinsically stable.

## 4.5 The Park Grass Experiment vs. the Ossekampen

It was laid out in Chapter 3, that the intrinsic stability of an ecosystem may be deducted from the extrinsic stabilities of identical systems in a range of climates (i.e. structured environmental fluctuations). The cutting and fertiliser regimes of the Park Grass Experiment are to some extent comparable to the cutting experiment of the Ossekampen. However, many other environmental variables (e.g. soil type) are different, which complicates a proper comparison of the extrinsic stabilities. Besides, observations under a larger range of climates would be required to enable extrapolation of the intrinsic stability. Table 4.8 lists the extrinsic variabilities of the plots in both experiments with comparable fertiliser regimes.

The emerging picture is unclear as three plots show a higher extrinsic variability in the Ossekampen experiment, i.e. the limed control, the PK-treatment and the NPK-treatment, whereas the N-treatment was more stable in the Ossekampen. The lack of consistent responses here may be explained by the small differences between the *structured* environmental fluctuations between the two climates, given by equation 3.5 in Chapter 3. Whereas the climate in the Park Grass Experiment

Table 4.8: Extrinsic variability of cut plots with comparable fertiliser treatments in the Park Grass Experiment and the Ossekampen.

| Fertiliser treatment | Extrinsic variability | |
|---|---|---|
| | Park Grass Experiment | Ossekampen |
| unlimed control | n.s. | 0.54 |
| limed control | 0.23 | 0.56 |
| unlimed N | 0.82 | 0.55 |
| unlimed PK | 0.45 | 0.68 |
| unlimed NPK | 0.34 | 0.49 |

showed structured rainfall and temperature variabilities of 0.13 and 0.51, respectively, the climate in the Ossekampen showed values of 0.13 and 0.58 respectively. Figure 3.4 in Chapter 3 showed that these differences in climate will only have a minor impact on the extrinsic variabilities of the ecosystems. Therefore it may be concluded that the differences between the extrinsic variabilities here may rather be caused by intrinsic ecosystem differences.

## 4.6 Discussion

*4.6.1 Limitations of the methodology*

The mathematical framework presented in Chapter 3 has been successfully applied to long-term experimental yield data, in order to derive the extrinsic variability of a range of grassland ecosystems from their temporal yield patterns. For most ecosystems studied in this paper, it has separated the effects of ecosystem management and of environmental noise on the system stability. Therefore it has enabled the testing of various hypotheses, derived from theoretical studies. Additionally, intrinsic ecosystem properties have been identified which regulate stability, yet have not been incorporated into grassland simulation models to date. Nevertheless, the limitations of this framework should be reflected in the interpretation of the results.

Firstly, the framework makes use of yields and environmental conditions during progressive decades, as a result of which the data are not mutually independent. Nevertheless, in Chapter 3 it was concluded that data of a large number of decades are required, in order to obtain significant relationships between the actual yield variability and the stochastic environmental variability. The six independent decades of the Park Grass Experiment for which data were available, were insufficient to elucidate these relationships. Therefore the use of progressive decades was a *sine qua*

*non* in the current study. Considering the mutual dependence of these progressive decades, however, the results of the multiple regressions should preferably be interpreted as indicators of stability only.

Secondly, all regressions assumed linear relationships between the actual yield variability and the stochastic environmental variability. The scarcity of "quiet" decades, i.e. decades with small temperature and rainfall differences between years, complicated the validation of alternative (e.g. quadratic) relationships. Moreover, this scarcity decreased the accuracy of the estimated extrinsic yield variability of each ecosystem, which was defined by the extrapolated Y-intercepts of the regressions. Nonetheless, low extrinsic variabilities were commonly found to be accompanied by positive sensitivities (regression slopes), whereas ecosystems with high extrinsic variabilities showed insignificant or negative sensitivities in all cases. These observations are in line with the model predictions made in Chapter 3 (Figure 3.3). Consequently, the stability levels of the observed ecosystems can be characterised with reasonable accuracy, by taking into account both the extrapolated extrinsic yield variability and the sensitivity.

Finally, in Chapter 3 it was demonstrated that even a mechanistically simulated ecosystem may show an actual yield variability which is to some extent unpredictable. As a result, the stochastic environmental variability, produced by the same simulation model, accounted for only part of the variance of the actual yield variability. The proportion of the variance accounted for by environmental fluctuations was consequently designated as the "predictability" of the simulated ecosystems. In contrast to these modelled ecosystems, however, the "real" ecosystems studied in the current paper were most likely subjected to a wide range of environmental variables, instead. Only two of these variables, i.e. the temperature and precipitation, have been used here to explain the yield variability of these real ecosystems. Therefore the variance accounted for in the regression in this study, does not only reflect the predictabilities of the ecosystems. Additionally it depends on whether all environmental variables, as well as their mutual interactions, have been properly included in the regression analysis. In spite of this uncertainty, again the observed predictabilities of extrinsically stable and unstable ecosystems matched closely to the predictabilities of their modelled counterparts in the previous Chapter (Chapter 3: Figure 3.3).

### *4.6.2 Stable and unstable ecosystems*

Clearly the concept of stability in grassland is ultimately complex, as it depends on the dynamic interplay between internal ecosystem properties, the management, the fertiliser regime, the climate, and on random environmental events. Hundreds of yield measurements are required to come to credible conclusions on the factors which stabilise and destabilise ecosystems. Although the field data discussed in this chapter leave many questions unanswered, the following universal processes appear to play an important role in grassland ecosystem stability.

Ecosystems under a cutting regime appeared to be extrinsically unstable. Both in the Park Grass Experiment (Figure 4.1) and the Ossekampen (Figure 4.6), the structured environmental fluctuations appeared to be not strong enough to stabilise these systems into extrinsically stable ecosystems. The cause of the extrinsic instability is not fully clear. Part of the internal fluctuations may be caused by the delayed nitrogen dependence of grasses on legumes, as discussed in Chapter 2, and as predicted by Thornley *et al.* (1995) and Schwinning & Parsons (1996a). However, plots receiving nitrogen, in which the delayed nitrogen dependence should not occur (Schwinning & Parsons, 1996a), were neither extrinsically stable, even though the extrinsic variability was lowest for the NPK plots in both experiments. In fact differences between fertiliser treatments were smaller than differences between liming treatment and management. Apparently other internal fluctuations play an important role, the nature of which needs to be elucidated. Thornley (1998) modelled a grass monoculture in a constant environment and found biennial yield fluctuations which were related to the interaction between plant and soil water status. Other conceivable delayed processes giving rise to internal fluctuations are the mutual dependence of species on other nutrients or trace elements, or maturity and reproduction processes (e.g. Dodd *et al.*, 1995).

In the Park Grass Experiment, ecosystems on soils with a high pH (limed plots) had a higher extrinsic variability than ecosystems on unlimed soils, which had been progressively acidified over time (Figure 4.1). The limed control plot in the Ossekampen showed an extrinsic variability similar to the unlimed control plot (Figure 4.6). However, the limed control had a lower (more negative) sensitivity than the unlimed plot, which resulted in a lower actual yield variability throughout the duration of the experiment.

Apparently the pH plays a crucial role in maintaining the stability of the ecosystem. In Chapter 2 it was suggested that a high pH may stimulate soil life and increase the nitrogen mineralisation rate. This would reduce the delay in nitrogen availability, and hence lead to an increased intrinsic stability. Indeed Bath *et al.* (1980) assumed that nitrogen mineralisation is reduced at pH levels below 4.5, while Rijtema & Koers (1991) suggest that these reductions occur at pH levels below 4.

The importance of soil processes was further confirmed by the lower extrinsic stability of the plot which received FYM, compared to the plot which received mineral nitrogen at approximately similar rates in the Park Grass Experiment (Figure 4.2). Part of the yield fluctuations could be explained by the four-yearly applications of FYM, as opposed to the yearly nitrogen applications on the fertilised plots (Figures 4.3 and 4.4). It remains unclear why these four-yearly yield fluctuations only occurred after 1960. It is conceivable that the changed methods of harvesting and yield measurements, from the weight of hay made to the dry matter weight of herbage at the hay-making

stage, led to a more accurate recording of yields, which allowed for the detection of the rather subtle four-yearly cycle.

In any case, even when the yields after 1960 were corrected for the effect of the four-yearly nutrient applications, the extrinsic stability of the FYM remained considerably lower than the stability of the fertilised plot (Figures 4.4 and 4.3), in spite of the assumed larger heterogeneity of the former. Silvertown (1980), studying the botanical equilibria in the Park Grass Experiment, found that the yields of plots which did not receive mineral nitrogen, showed a more pronounced response to spring rainfall, than the yields of plots under a nitrogen regime. He suggested that the herbage production on the unfertilised plots was depended on the nitrogen mineralisation rate, which in turn was dependent on rainfall. In the current analysis, the yields of the FYM plot indeed showed a stronger response to the rainfall during the growing season than the yields of the fertilised plot (not shown). Therefore the soil processes involved in the mineralisation of the organic nitrogen arguably had a larger impact on the stability of the FYM plot, than the spatial heterogeneity, which was assumed to have arisen from the FYM dressings. These findings further emphasise the large impact of the soil processes on the ecosystem stability.

Interestingly, soil processes have received little attention in grassland simulation models to date (e.g. Parsons *et al.*, 1991b; Thornley *et al.*, 1995; Schwinning & Parsons, 1996a). Although Thornley's (1998) model of a grass monoculture contains a more detailed account of soil processes, these are assumed to be independent of the acidity of soils. The evidence from the Park Grass Experiment presented here, instead suggests that it is mandatory to include the acidifying and alkalifying soil processes into grassland simulation models, as well as their impacts on mineralisation rates.

The management of grassland ecosystems also has a crucial impact on their stability. The permanently grazed systems in the Ossekampen experiment (Figure 4.7) showed much lower extrinsic variabilities than their cut counterparts (Figure 4.6). This higher stability could be related to a range of factors.

Firstly, the average biomass on the grazed plots may be expected to have been lower than the average biomass on the plots which were cut twice yearly. This will have reduced the probability of species fully shading each other, and therefore this may have reduced the competition for light. In Chapter 2 this light competition was shown to destabilise ecosystems.

Secondly, if species with lower production levels had escape mechanisms from grazing, grazing will have lead to a proportionally larger animal intake of the taller, i.e. most productive species, thereby stabilising the mixture (Chapter 2).

Thirdly, the intake of legume tissue by animals, and the excretion of excess nitrogen will

have lead to an accelerated recycling of nutrients (Schwinning & Parsons, 1996a). This will have reduced the time-delay between nitrogen fixation by the legumes and its availability to the other species. The delayed nitrogen dependence in the cut plots may have been responsible for a large share of the intrinsic instability of ecosystems under a cutting regime.

Finally, cutting is a "sweeping event" (Chapter 2), which sets the development of all plants within each plot "in phase". Therefore all these plants and species may be expected to show identical intrinsic fluctuations. Moreover, it is conceivable that all species respond in similar manners to environmental events. In contrast, grazing leads to local tissue removals and faeces and urine depositions, which are all "buckshot events". It was shown in Chapter 2 that these buckshot events may set patches "out of phase", which means that these patches may compensate for each other in respect to their intrinsic fluctuations and to environmental events.

In summary, to date the intrinsic stability properties of ecosystems has mainly been studied using simulated, i.e. modelled ecosystems. In field experiments, these intrinsic properties are commonly "obscured" by environmental noise. The mathematical framework presented in Chapter 3 provides an analytical tool to "filter" this environmental noise from yield patterns of long-term experiments. Herewith it allows for a genuine comparison of the extrinsic stability properties of "real" ecosystems.

In theoretical studies of mixed ecosystems, instability has mainly been related to the destabilising effects of the inter-species competition for light (e.g. Parsons *et al.*, 1991b; Chapter 2), and of delayed nitrogen dynamics (e.g. Thornley *et al.*, 1995; Schwinning & Parsons, 1996a; Chapter 2). Instead, plant escape mechanisms from grazing (e.g. Noy-Meir, 1975, Parsons *et al.*, 1991b, Schwinning & Parsons, 1996a, Chapter 2) and the spatial heterogeneity resulting from grazing (Schwinning & Parsons, 1996b), have been identified to stabilise mixed ecosystems. Although these findings are not contradicted by the new analysis of the yield patterns of the real ecosystems in the Park Grass Experiment and the Ossekampen, presented in this chapter, the results from this study suggest that soil processes, in particular pH-dependent soil processes, and the grassland management have an overriding effect on ecosystem stability.

Considering the large number of grassland ecosystems in the Park Grass Experiment and the Ossekampen, which have not been analysed in this study, and taking into account the existence of other long-term grassland experiments across Europe, many more intrinsic ecosystem properties and processes could be readily identified, by using the mathematical framework of this study. When identical ecosystems are identified in a range of climates, the intrinsic stability level of each of these systems may also be quantified, in addition to their extrinsic stability level.

Finally, in Chapter 2 it was tentatively suggested that grassland ecosystems share features with forest ecosystems. The application of the current framework is not necessarily restricted to

grassland ecosystems. Instead, its application to other types of ecosystems would indeed be an interesting challenge.

## Acknowledgements

The author is much indebted to Dr. Paul Poulton of Rothamsted Experimental Station, Rothamsted, UK, and to Mr. Thies Oomes of Plant Research International, Wageningen, The Netherlands, for their kind permission to use the databases of the Park Grass Experiment and the Ossekampen, respectively, without which this study would not have been possible. The author is also very grateful to Dr. Adrie Jacobs of the Department of Meteorology and Air Quality, Wageningen University, The Netherlands, for kindly providing the meteorological data of the Ossekampen experiment.

# Part II:

# Spatial aspects of grassland stability

# Chapter 5: Mechanistic simulation of the vertical structure of mixed swards

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## Abstract

1) The vertical structure is an important feature of mixed swards, as it influences the inter-species competition for light, as well as the patterns of grazing. Although the experimental measurement of the vertical sward structure is relatively straight-forward, the mechanistic and dynamic modelling of the bulk density and lamina density profiles is complicated by the unpredictability of leaf angles. Therefore only static, descriptive profiles have been incorporated in grassland simulation models to date.

2) Two mechanistic models are presented which predict the bulk density profiles and the lamina density profiles of perennial ryegrass and white clover, based on variables which can readily be measured or produced by simulation models.

3) The "basic model" for grass requires only three input variables: the average leaf length, the average sheath length, and either the total herbage mass or the Leaf Area Index. For clover, only the average petiole length, and either the total weights or areas of petiole and lamina material are required. Use of this basic model is restricted to the simulation of homogeneous swards in which all herbage material shows a random spatial orientation.

4) The "extended model" is more flexible and capable of simulating a wide range of different sward types. However, it requires variables which have not been produced by simulation so far, such as the distributions of leaf top heights, sheath top heights, and petiole top heights.

5) Both models were evaluated against a measured profile of a grass-clover sward. The bulk density and lamina density profiles of both perennial ryegrass and white clover, as predicted by the extended model, closely matched the observed profiles. However, the predictions of the basic model were significantly inaccurate for both ryegrass and clover.

6) The extended model can be incorporated as a sub-model into dynamic grassland simulation models, in order to enhance the accuracy of simulation of both competition for light and of grazing.

## 5.1 Introduction

Over the past two decades grass growth has been simulated dynamically by various physiological and morpho-physiological simulation models, in which grass growth is determined by light, temperature, nitrogen, or a combination of these factors (Thornley & Verberne, 1989; Parsons *et al.*, 1991b; Van Loo, 1993; Thornley, 1998). Although some of these models incorporate descriptions of grass morphology, the vertical bulk density and lamina density distributions are usually simplified, and simulated statically, by using profiles with fixed shapes for the duration of the simulation. It can be argued that the vertical lamina density profile is only of minor importance to the $CO_2$ assimilation of grassland monocultures, in which all intercepted radiation is absorbed by the one species, regardless of the vertical distribution of its leaves. Yet in mixtures of grassland species, and particularly in mixtures of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*), the heights of assimilatory leaf material of both species is decisive in the competition for light (Lantinga *et al.*, 1999). In mixed swards, differences in these heights can lead to asymmetric light competition, in which one species progressively overshadows its companion species (Nassiri, 1998).

Additionally, the grazing characteristics and the ingested diet are also dependent on the vertical sward structure. The herbage intake rate is a function of sward properties such as the vertical and horizontal dispersion of plant material, as well as of animal properties such as bite area, bite depth, handling time and maximum grazing time (e.g. Parsons *et al.*, 1994; Brereton & McGilloway, 1999). Brereton & McGilloway (1999) successfully simulated grazing of a ryegrass monoculture by assuming that grazing animals show a within-species selectivity for lamina material over sheath material in the available sward layer. Parsons *et al.* (1994) found that in mixtures of grass and clover, the animal's desire to maximise clover intake may be compromised by the requirement to optimise total energy intake, depending on both the lateral and vertical structure of the sward.

Even though the experimental measurement of the bulk density and lamina density profiles of both perennial ryegrass and white clover is relatively straightforward (Nassiri, 1998; Lantinga *et al.*, 1999), the analysis and the mechanistic modelling of the vertical sward structure are complicated by the limited predictability of leaf and petiole angles. Direct measurements of these angles are labourious, and only few examples can be found in the literature (e.g. De Wit, 1965; Coughenour, 1984; Gibson *et al.*, 1992).

As a consequence, most dynamic grassland simulation models simply assume either a uniform vertical distribution of lamina material from ground level to sward surface (e.g. Parsons *et al.*, 1991b) or log-normal distributions (e.g. Coughenour *et al.*, 1984). Parsons *et al.* (1994) used a

symmetric parabola and a skewed parabola to describe the vertical lamina density distributions of perennial ryegrass and clover, respectively. Even the comprehensive ecosystem simulation model of Thornley (1998), containing a detailed simulation of leaf $CO_2$ assimilation, uses a uniform distribution for perennial ryegrass. In fact, uniform distributions are in conflict with observations by Milne *et al.* (1982), Parsons *et al.* (1988), Parsons *et al.* (1991a), Nassiri (1998) and Lantinga *et al.* (1999), who all empirically established non-uniform vertical lamina distributions of perennial ryegrass and white clover. Nassiri (1998) and Lantinga *et al.* (1999) fitted their observed lamina density profiles with triangular density functions, in which the height of the maximum lamina density was strongly correlated to the plant height. Additionally, they used a variable extinction coefficient for different sward layers, which depended on the leaf dispersion within these layers. This enabled accurate simulation of light interception throughout the sward profile. However, their approach presumed triangularly shaped lamina density profiles of both grass and clover, which may only apply to a limited range of sward types. All swards of their study were subjected to a cutting regime, and different profiles and different relations between plant height, maximum lamina density height, and leaf dispersion may be expected under a grazing regime or under a management regime of alternating cutting and grazing.

In conclusion, the vertical sward structure defines both the light interception of mixed pastures, and grazing factors such as bite depth, handling time, and the selectivity between and within species by the animals. Current pasture simulation models show detailed accounts of both grazing and $CO_2$ assimilation processes (e.g. Parsons *et al.*, 1994; Thornley, 1998; Brereton & McGilloway, 1999). Nevertheless, the vertical sward profiles used for these simulations are either simplified (e.g. Thornley, 1998), observed (e.g. Brereton & McGilloway, 1999), static (e.g. Parsons *et al.*, 1994), or limited to a particular pasture management (Nassiri, 1998; Lantinga *et al.*, 1999). The development of accurate simulation models which are capable of dynamic simulation of mixed swards under a range of management regimes, requires a sub-model which dynamically predicts the amounts of lamina, sheath, and bulk of each species over the full vertical profile, based on input-variables which can be produced by the overall simulation model.

This chapter presents such a mathematical model predicting the vertical distributions of lamina material and of the total leaf material of both perennial ryegrass and white clover. For the simulation of a perennial ryegrass sward in which the leaves show a random spatial orientation, the only input variables required are the mean leaf length, the mean sheath length and either the total dry matter yield or the total leaf area index. These variables can already be produced by dynamic grassland simulation models (e.g. Van Loo, 1993). The present model can calculate the vertical sward profiles, as affected by growth and grazing, for any moment during the simulation period. This

"basic model" is then extended to account for variation of the leaf and sheath length, and to enable simulation of swards which show a prevailing orientation of leaf material. Finally, modifications of both models are presented which mechanistically predict the same profiles for white clover.

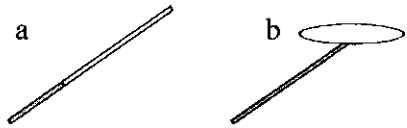


Figure 5.1: Assumed morphology of a) a perennial ryegrass leaf, b) a white clover leaf, as used by the basic and extended models. Shaded areas: sheath (ryegrass) / petiole (clover), white areas: lamina.

## 5.2 The basic model (perennial ryegrass)

The basic model simulates the vertical sward structure of a homogeneous vegetative perennial ryegrass sward. The presence of generative tillers is disregarded. It is assumed that there is no variation in leaf lengths or sheath lengths, and that leaf area and leaf weight are both uniformly distributed over the full length of the leaf. As a result any possible differences between the specific areas (area per unit mass) of lamina and sheath are neglected. All leaves are considered linear and stiff, the lower part consisting of sheath material and the top part of lamina material (Figure 5.1a). Most important, *pro tem.* leaf angles are assumed to be random in three dimensions. Although this is a major simplification, it appears to be a better first order approximation than the assumption of the constant leaf angle which leads to the often assumed uniform leaf area distributions (Goudriaan, 1988).

### *5.2.1 Simulation of the vertical leaf area and bulk density distribution*

From the assumptions above it follows that the leaf tops will be equally distributed on the surface of a virtual hemisphere with a radius equal to the total leaf length $\lambda_{leaf}$ (m) (Figure 5.2a). Therefore, the vertical distribution of the leaf tops is identical to the vertical distribution of the hemisphere surface. This surface is uniformly distributed over the height of the hemisphere, as the decreasing circumference of latitudes at the top of the hemisphere is fully compensated by the increasingly horizontal orientation of the surface. Consequently, with random leaf angles, the leaf tops show a uniform vertical distribution from ground level to the maximum leaf height ($\lambda_{leaf}$).

Let $h$ (m) be the measuring height, i.e. the height under which the total cumulative leaf area is calculated. Let $x$ (m) be the height of the top of an individual leaf, and $f_h$ (no dimension) the fraction of this leaf which is located under measuring height $h$. If the leaf top appears under height $= h$, then $f_h = 1$, i.e. the entire leaf is located under the height of measuring. From Figure 5.2b it follows that for leaves with their tops higher than height $= h$:

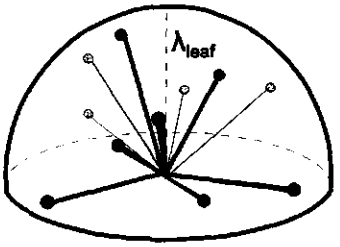


Figure 5.2a: The basic model assumes that the leaf tops are uniformly distributed on the surface of a hypothetical hemisphere with radius $\lambda_{leaf}$.

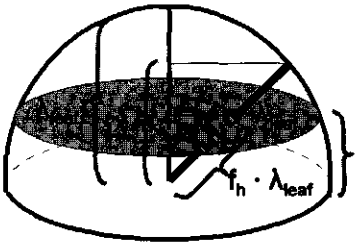


Figure 5.2b: $f_h$ is the fraction of an individual leaf that is located under the measuring height *h*. The leaf length is $\lambda_{leaf}$ and the leaf top height is x.

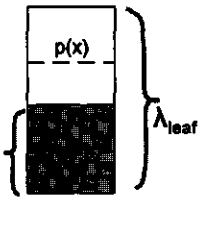


Figure 5.2c: The probability of a leaf top occurring under *h* (shaded area) and the probability density of a leaf top occurring at a particular height between *h* and $\lambda_{leaf}$ (dashed line), assuming a uniform distribution of leaf tops across the maximum height of the sward.

$$f_h = \frac{h}{x} \qquad \text{Eq. 5.1}$$

The probability of a leaf top appearing under the measuring height is given by $P(x<h)$. For uniform distributions of leaf top heights (Figure 5.2c), this probability is given by :

$$P(x<h) = \frac{h}{\lambda_{leaf}} \qquad \text{Eq. 5.2}$$

The probability density of a leaf top appearing at any height between *h* and $\lambda_{leaf}$ is given by the probability density function p(x). Since x is uniformly distributed between $x = 0$ and $x = \lambda_{leaf}$, this function p(x) is given by:

$$p(x) = \frac{1}{\lambda_{leaf}} \qquad \text{Eq. 5.3}$$

At large numbers of leaves, the expectation value of $f_h$ represents the *cumulative* fraction *V(h)* (no dimension) of the mass or the leaf area under height *h*. This expectation value $E(f_h)$ can be derived from the products of the fractions $f_h$ and the probabilities of the corresponding leaf top heights:

$$V(h) = E(f_h) = 1 \cdot P(x<h) + \int_{x=h}^{\lambda_{leaf}} f_h \cdot p(x)\, dx \qquad \text{Eq. 5.4}$$

Substitution of equations 5.2, 5.3 and 5.1 into equation 5.4 gives:

$$V(h) = \frac{h}{\lambda_{leaf}} + \int_{x=h}^{\lambda_{leaf}} \frac{h}{\lambda_{leaf}} \cdot \frac{1}{x}\, dx \qquad \text{Eq. 5.5}$$

This integral can be solved algebraically, resulting in:

$$V(h) = \frac{h}{\lambda_{leaf}} - \frac{h}{\lambda_{leaf}} \cdot \ln\left(\frac{h}{\lambda_{leaf}}\right) \qquad \text{Eq. 5.6}$$

The leaf weight $W_{leaf\,1\text{-}2}$ (g m$^{-2}$) and the leaf area $L_{leaf\,1\text{-}2}$ (m$^2$ m$^{-2}$) in the sward layer from height = $h_1$ to height = $h_2$ is now given by:

$$W_{leaf\,1\text{-}2} = [\, V(h_2) - V(h_1) \,] \cdot W_{leaf\,tot} \qquad \text{Eq. 5.7a}$$

and:

$$L_{leaf\,1\text{-}2} = [\, V(h_2) - V(h_1) \,] \cdot L_{leaf\,tot} \qquad \text{Eq. 5.7b}$$

respectively, in which $W_{leaf\,tot}$ and $L_{leaf\,tot}$ are the total weight and the total leaf area of the crop.

*5.2.2 Simulation of the lamina distribution*

Subsequently, lamina and sheath material within the leaves are discriminated, in order to obtain the vertical lamina distribution profile. Some authors (e.g. Van Loo, 1993) ignore differences between laminae and sheaths, and simulate the assimilatory activity of entire leaves only. Others (e.g. Parsons *et al.*, 1991b) assume that $CO_2$ assimilation is restricted to the lamina. Coughenour *et al.* (1984) simulate $CO_2$ assimilation by attributing sheaths with a assimilatory capacity of a fifth of the lamina activity. Either way, it is essential to discriminate the vertical lamina distribution from the vertical distribution of entire leaves. Apart from this, Brereton & McGilloway (1999) showed that the fraction of the herbage in a sward layer consisting of lamina material determines the quantity and quality of grazing and of the animal diet.

The simulated leaves are assumed to be linear and stiff, and to consist of two components:

sheath material at the lower part, and lamina material at the top part (Figure 5.1a). As a result all sheaths are, similarly to the entire leaves, considered to have identical lengths, to be stiff and linear, and to be distributed randomly in three dimensions. Therefore the vertical distribution of sheath material can be obtained by using the same equations used for the vertical leaf distribution, substituting $\lambda_{leaf}$ with the mean sheath length $\lambda_{sheath}$, and $W_{leaf\,tot}$ and $L_{leaf\,tot}$ with the total sheath weight and sheath area, $W_{sheath\,tot}$ and $L_{sheath\,tot}$, respectively. The lamina mass in the layer from $h_1$ to $h_2$, $W_{lam\,1\text{-}2}$ (g $m^{-2}$) is then given by the difference between the total leaf mass ($W_{leaf1\text{-}2}$) and the sheath mass ($W_{sheath1\text{-}2}$) in this layer:

$$W_{lam\,1\text{-}2} = W_{leaf\,1\text{-}2} - W_{sheath\,1\text{-}2} \qquad \text{Eq. 5.8a}$$

And the same procedure applies to the lamina area in this layer $L_{lam\,1\text{-}2}$ ($m^2$ $m^{-2}$), using an obvious notation:

$$L_{lam\,1\text{-}2} = L_{leaf\,1\text{-}2} - L_{sheath\,1\text{-}2} \qquad \text{Eq. 5.8b}$$

The required values of the new input variables $\lambda_{sheath}$, $W_{sheath\,tot}$ and $L_{sheath\,tot}$ can either be measured directly, obtained from simulation, or assumed to be a constant fraction of the total leaf length, leaf weight and leaf area, respectively. Parsons *et al.* (1991a) found that the incremental sheath weight ratio was constant at 0.35 for perennial ryegrass, irrespective of total leaf size. The actual sheath weight ratio will obviously increase under a grazing regime, when lamina weight and length are progressively reduced.

## 5.3 The extended model (perennial ryegrass)

The transparent structure of the basic model is the result of two major simplifications, the assumptions that a) the leaf tops and sheath tops are uniformly distributed over the height, and b) all leaves and sheaths have equal lengths. Nevertheless a wide range of grassland conditions is conceivable in which these assumptions may not apply. In grazed swards, a considerable variation in leaf lengths may be expected. Schulte (unpublished data) found that grass seedlings orientate their leaves vertically for a limited period of time. De Wit (1965) also found mostly erect leaves in silage swards after a cutting event. In contrast, a mainly horizontal orientation of the herbage was observed in heavy, lodging swards. Therefore the basic model is extended to account for a) dispersion of leaf lengths, and b) a prevailing orientation of lamina and sheath material (Figure 5.3a).

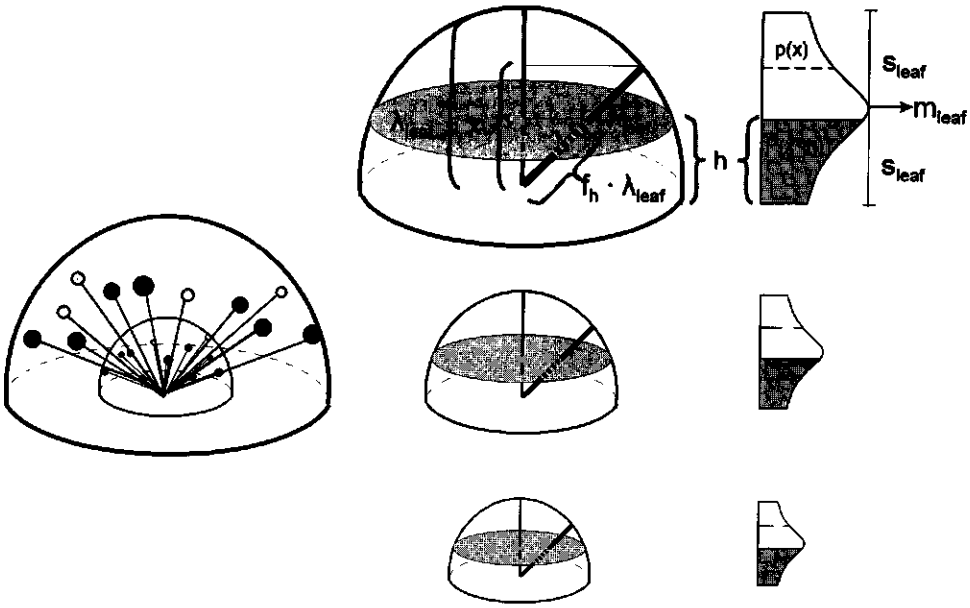


Figure 5.3a: The extended model caters for swards in which leaves show a prevailing spatial orientation and differ in lengths.

Figure 5.3b: The extended model groups leaves into leaf length classes, three of which are illustrated. Classes are treated identically. Legend as in figure 2b.

Figure 5.3c: The extended model assumes that within each leaf length class, leaf top heights show a normal distribution. Legend as in figure 2c.

### *5.3.1 Leaf length variation*

The assumption of the basic model that all leaves have equal lengths is now replaced by the assumption that the leaf length is normally distributed with a mean value of $\mu_{leaf}$, and with a standard deviation of $\sigma_{leaf}$. The maximum leaf length is arbitrarily set at 0.4 m. If preferred, an other value can be applied. This maximum length is required as otherwise the normal distribution will give a probability, however small, to unrealistically large leaf lengths. The frequency density function $\phi(\lambda_{leaf})$ of leaf lengths is given by the frequency density function of a normal distribution with a mean value of $\mu_{leaf}$ (m), and with a standard deviation of $\sigma_{leaf}$ (m):

$$\phi(\lambda_{leaf}) = \frac{1}{\sigma_{leaf}\sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{\lambda_{leaf} - \mu_{leaf}}{\sigma_{leaf}}\right)^2} \qquad \text{Eq. 5.9}$$

In the extended model, leaves are grouped into virtual leaf length classes, the boundaries of which are infinitively narrow, and which are treated identically. First each class is allocated with a fraction of the total leaf area and leaf weight. Next the vertical distributions of each class are

calculated separately, and subsequently the distributions of all classes are integrated.

*5.3.2 Mass and area allocation between classes*

Obviously, large leaves contribute more mass and area to the total vertical structure than do small leaves. Here it is assumed that the relative contribution of each leaf length class $C(\lambda_{leaf})$ (no dimension) is linearly related to a) the frequency density of the leaf length class $\phi(\lambda_{leaf})$ (equation 5.9), and to b) the leaf length, relative to the sum of all leaf lengths:

$$C(\lambda_{leaf}) = \phi(\lambda_{leaf}) \cdot \frac{\lambda_{leaf}}{\int_{\lambda_{leaf}=0}^{0.4} \lambda_{leaf} \cdot \phi(\lambda_{leaf})\, d\lambda_{leaf}} \qquad \text{Eq. 5.10a}$$

The assumed linear relationship between the contribution and the leaf length presupposes that the leaf width is constant for all leaf length classes. If preferred, the leaf width may be assumed to increase in larger leaves, which would lead to a quadratic relationship between the contribution and the leaf length of each class:

$$C(\lambda_{leaf}) = \phi(\lambda_{leaf}) \cdot \frac{\lambda_{leaf}^2}{\int_{\lambda_{leaf}=0}^{0.4} \lambda_{leaf}^2 \cdot \phi(\lambda_{leaf})\, d\lambda_{leaf}} \qquad \text{Eq. 5.10b}$$

*5.3.3 Non-uniform leaf and sheath top distributions within classes*

The assumption of random leaf angles in the basic model resulted in the uniform distribution of both leaf tops and sheath tops. The extended model assumes that the leaves and sheaths show a prevailing orientation, which is identical for all leaf length classes. It is assumed that *within each class of leaf lengths*, the leaf top height x is normally distributed with a mean equal to $m_{leaf} \cdot \lambda_{leaf}$ and a standard deviation equal to $s_{leaf} \cdot \lambda_{leaf}$ (Figure 5.3c). $m_{leaf}$ (m m$^{-1}$) and $s_{leaf}$ (m m$^{-1}$) are constants representing the average leaf top height, and the standard deviation of the leaf top height, expressed relatively to the leaf length. Note that the leaf top height distribution of the entire crop differs from leaf top height distribution of each class, as the former is also dependent on the distribution of leaf lengths. The probability that a leaf with length $\lambda_{leaf}$ is entirely located under the measuring height, i.e. P (x<h) (eq. 5.2) is now replaced by:

$$P(x<h) = \frac{\int_{x=0}^{h} \frac{1}{s_{leaf} \cdot \lambda_{leaf} \sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{x - m_{leaf} \cdot \lambda_{leaf}}{s_{leaf} \cdot \lambda_{leaf}}\right)^2} dx}{\int_{x=0}^{\lambda_{leaf}} \frac{1}{s_{leaf} \cdot \lambda_{leaf} \sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{x - m_{leaf} \cdot \lambda_{leaf}}{s_{leaf} \cdot \lambda_{leaf}}\right)^2} dx} \qquad \text{Eq. 5.11}$$

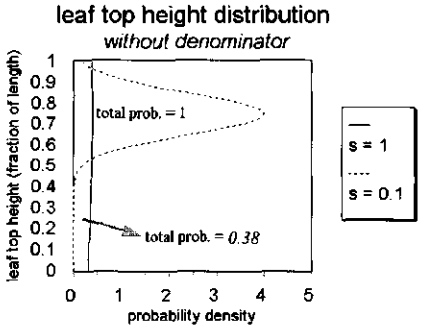


Figure 5.4a: Two hypothetical leaf top height probability density functions (equation 5.11 without denominator). Solid line: large variation of leaf top heights, $s_{leaf}$ = 1, dashed line: small variation of leaf top heights $s_{leaf}$ = 0.1. As the first distribution also returns probabilities to leaf top heights either > 1 or < 0, the total probability of realistic leaf top heights between 0 and 1 times the leaf length, is only 0.38.

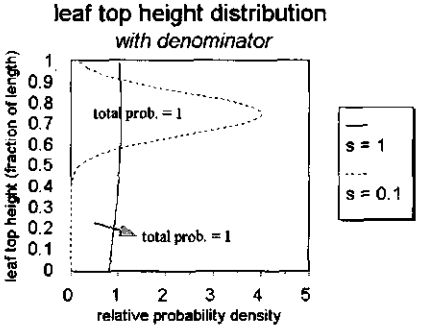


Figure 5.4b: Both functions have been divided by the probability of realistic leaf top heights, i.e. leaf top heights between 0 and 1 times the leaf length, to yield the relative probability density functions (equation 5.11). The total relative probability of realistic leaf top heights now equals 1 for both functions.

in which the denominator is a premultiplier giving the total probability of a leaf top height between 0 and $\lambda_{leaf}$. Its value is smaller than 1 and depends on the values of $m_{leaf}$ and $s_{leaf}$, as the normal distribution itself will return unrealistic leaf top heights smaller than 0 and higher than $\lambda_{leaf}$ for a certain amount of leaves. Therefore the probability of leaf tops under height $h$ is expressed as a fraction of all realistic leaf top heights. The above is exemplified in Figure 5.4.

Similarly, the probability density function of leaf top heights between $h$ and $\lambda_{leaf}$ in equation 5.3 is replaced by:

$$p(x) = \frac{\frac{1}{s_{leaf} \cdot \lambda_{leaf} \sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{x - m_{leaf} \cdot \lambda_{leaf}}{s_{leaf} \cdot \lambda_{leaf}}\right)^2}}{\int_{x=0}^{\lambda_{leaf}} \frac{1}{s_{leaf} \cdot \lambda_{leaf} \sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{x - m_{leaf} \cdot \lambda_{leaf}}{s_{leaf} \cdot \lambda_{leaf}}\right)^2} dx} \qquad \text{Eq. 5.12}$$

Note that p(x) returns to a uniform probability density function for $s_{leaf} \Rightarrow \infty$.

Identically to the basic model, $f_h$ is the fraction of an individual leaf with length $\lambda_{leaf}$ with leaf top height $x$, that is located under the measuring height $h$, and defined by $h / x$ (eq. 5.1). The expectation value of $f_h$, represented by $E(f_h)$ (no dimension), is again the mean *fraction* of the leaves of this leaf length class that is located under measuring height $h$ (eq. 5.4), and is given by $F(h)$ (no dimension):

$$F(h) = E(f_h) = 1 \cdot P(x<h) + \int_{x=h}^{\lambda_{leaf}} f_h \cdot p(x)\, dx \qquad \text{Eq. 5.13}$$

In the extended model, the terms are substituted with equations 5.11, 5.1, and 5.12, respectively.

*3.4 Total vertical leaf area and leaf mass distributions* .

The cumulative fraction of leaf material of *all* classes of leaf lengths under measuring height *h*, *V(h)* (no dimension), is now derived by integrating the product of the leaf fraction under measuring height *h* of individual classes, and the area / mass contribution of each leaf length class:

$$V(h) = \int_{\lambda_{leaf}=0}^{0.4} F(h) \cdot C(\lambda_{leaf})\, d\lambda_{leaf} \qquad \text{Eq. 5.14}$$

Its terms are can consequently be substituted with equations 5.13 and 5.10a, respectively. This equation cannot be solved algebraically, yet it can be approached by numerical iteration.

The leaf weight $W_{leaf\ 1\text{-}2}$ (g $m^{-2}$) and the leaf area $L_{leaf\ 1\text{-}2}$ ($m^2$ $m^{-2}$) in the sward layer from height = $h_1$ to height = $h_2$ is now given by (compare with equations 5.7a and 5.7b):

$$W_{leaf\ 1\text{-}2} = [\ V(h_2) - V(h_1)\ ] \cdot W_{leaf\ tot} \qquad \text{Eq. 5.15a}$$

and:

$$L_{leaf\ 1\text{-}2} = [\ V(h_2) - V(h_1)\ ] \cdot L_{leaf\ tot} \qquad \text{Eq. 5.15b}$$

The same procedure is repeated for the sheaths, and the vertical lamina density distribution and the vertical lamina weight distribution are obtained following equations 5.8a and 5.8b of the basic model.

## 5.4 Modification of the basic and the extended model for white clover

The morphology of white clover leaves differs largely from the morphology of perennial ryegrass leaves. Therefore simulation of the bulk density, lamina density and lamina fraction profiles of white clover requires modification to the equations presented above. White clover leaves consist of two components: the petiole and the lamina. In contrast to the lamina material of ryegrass, the

clover lamina is located entirely at the top of the petiole, and assumed to show a fully horizontal orientation (Figure 5.1b). The "folded" lamina of growing clover leaves (Parsons *et al.*, 1991a) is ignored here.

*5.4.1 The basic model (white clover)*

For perennial ryegrass, the vertical distributions of entire leaf material and of sheath material were calculated first, and the lamina distribution was obtained by the difference between these in each sward layer. For clover, the order is reversed: first the distributions of petiole material and lamina material are calculated, after which the distribution of entire clover leaves is given by the sum of these.

**Distribution of petiole material**

The basic model for white clover assumes that all petioles are of the same length $\lambda_{Tr\,pet}$ (m), and that these petioles show a random spatial orientation. As a result, in the basic model the petiole tops will show the same uniform vertical frequency density distributions as the leaf tops of perennial ryegrass. The cumulative fraction of petiole material $V(h)$ (no dimension) can then be calculated similarly to the vertical sheath density profile of perennial ryegrass, i.e. by replacing $\lambda_{leaf}$ with $\lambda_{Tr\,pet}$, and $W_{sheath\,tot}$ with the total petiole mass $W_{Tr\,pet\,tot}$, and $L_{sheath\,tot}$ with $L_{Tr\,pet\,tot}$, in equations 5.1 to 5.7, resulting in (compare with equations 5.6 and 5.7):

$$V(h) = \frac{h}{\lambda_{Tr\,pet}} - \frac{h}{\lambda_{Tr\,pet}} \cdot \ln\left(\frac{h}{\lambda_{Tr\,pet}}\right) \qquad \text{Eq. 5.16}$$

$$W_{Tr\,pet\,1\text{-}2} = \left[ V_{Tr\,pet}(h_2) - V_{Tr\,pet}(h_1) \right] \cdot W_{Tr\,pet\,tot} \qquad \text{Eq. 5.17a}$$

$$L_{Tr\,pet\,1\text{-}2} = \left[ V_{Tr\,pet}(h_2) - V_{Tr\,pet}(h_1) \right] \cdot L_{Tr\,pet\,tot} \qquad \text{Eq. 5.17b}$$

**Distribution of lamina material**

The assumed horizontal orientation of all clover lamina material in fact means that all lamina material of a single leaf is located at the same height as the petiole top. The fraction of the lamina material under measuring height $h$ will then be identical to the fraction of petiole tops under this height (compare equation 5.2 of the basic model for perennial ryegrass):

$$V(h) = P(x<h) = \frac{h}{\lambda_{Tr\ pet}} \qquad \text{Eq. 5.18}$$

The lamina mass $W_{Tr\ lam\ 1\text{-}2}$ (g m$^{-2}$) and lamina area $L_{Tr\ lam\ 1\text{-}2}$ (m$^2$ m$^{-2}$) in the sward layer between heights $h_1$ and $h_2$ are then given by:

$$W_{Tr\ lam\ 1\text{-}2} = [\ V(h_2) - V(h_1)\ ] \cdot W_{Tr\ lam\ tot} \qquad \text{Eq. 5.19a}$$

$$L_{Tr\ lam\ 1\text{-}2} = [\ V(h_2) - V(h_1)\ ] \cdot L_{Tr\ lam\ tot} \qquad \text{Eq. 5.19b}$$

in which $W_{Tr\ lam\ tot}$ (g m$^{-2}$) and $L_{Tr\ lam\ tot}$ (m$^2$ m$^{-2}$) are the total lamina weight and area of clover, respectively.

**Distribution of total clover material**

The total leaf weight and area of clover in the sward layer between heights $h_1$ and $h_2$, $W_{Tr\ leaf\ 1\text{-}2}$ (g m$^{-2}$) and $L_{Tr\ leaf\ 1\text{-}2}$ (m$^2$ m$^{-2}$), are now simply given by the sum of the petiole and lamina weights and by the sum of the petiole and lamina areas in this layer, respectively, adding equations 5.17a and 5.19a, and equations 17b and 19b:

$$W_{Tr\ leaf\ 1\text{-}2} = W_{Tr\ pet\ 1\text{-}2} + W_{Tr\ lam\ 1\text{-}2} \qquad \text{Eq. 5.20a}$$

$$L_{Tr\ leaf\ 1\text{-}2} = L_{Tr\ pet\ 1\text{-}2} + L_{Tr\ lam\ 1\text{-}2} \qquad \text{Eq. 5.20b}$$

*5.4.2 The extended model (white clover)*

**Distribution of petiole material**

The extended model assumes that the lengths of the petioles show a normal distribution with a mean petiole length $\mu_{Tr\ pet}$ (m) and a standard deviation $\sigma_{Tr\ pet}$ (m). The random spatial orientation of petioles is replaced by a normal distribution of the petiole top heights *within* each petiole length class, with mean values $m_{Tr\ pet} \cdot \lambda_{Tr\ pet}$ (m) and standard deviation $s_{Tr\ pet} \cdot \lambda_{Tr\ pet}$ (m). Hence the clover petioles are treated similar to the leaves of the ryegrass. The vertical distribution of petiole material can therefore be obtained by using the same equations 5.9 to 5.15b of the extended model for

perennial ryegrass. However, for clover it is assumed that the width of the petiole does increase with larger petiole lengths. Therefore the quadratic relationship is presupposed between the contribution and the petiole length of each petiole length class (equation 5.10b).

**Distribution of lamina material**

Similar to the basic model for white clover, all lamina material of each leaf is assumed to be located at the same height as its petiole top. Therefore, within each petiole length class, the fraction of lamina material located under the measuring height *h*, *F(h)* (no dimension), is equal to the probability of a petiole top appearing under this height, as given by equation 5.11 of the extended model for perennial ryegrass:

$$F(h) = P(x<h) = \frac{\int_{x=0}^{h} \frac{1}{s_{Tr\ pet} \cdot \lambda_{Tr\ pet} \sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{x - m_{Tr\ pet} \cdot \lambda_{Tr\ pet}}{s_{Tr\ pet} \cdot \lambda_{Tr\ pet}}\right)^2} dx}{\int_{x=0}^{\lambda_{Tr\ pet}} \frac{1}{s_{Tr\ pet} \cdot \lambda_{Tr\ pet} \sqrt{2\pi}} \cdot e^{-\frac{1}{2}\left(\frac{x - m_{Tr\ pet} \cdot \lambda_{Tr\ pet}}{s_{Tr\ pet} \cdot \lambda_{Tr\ pet}}\right)^2} dx} \qquad \text{Eq. 5.21}$$

Consequently, for *all* petiole length classes, the cumulative fraction of lamina material under the measuring height *h*, *V(h)* (no dimension) is given by equation 5.14 of the extended model for perennial ryegrass, substituting its terms with equations 5.13 and 5.10b, respectively. The total lamina weight and lamina area in the sward layer from $h_1$ to $h_2$, $W_{Tr\ lam\ 1\text{-}2}$ (g $m^{-2}$) and $L_{Tr\ lam\ 1\text{-}2}$ ($m^2$ $m^{-2}$), are given by equations 5.19a and 5.19b, respectively.

**Distribution of total clover material**

Similar to the basic model for clover, the total leaf weight and area of clover in the same layer are given by equations 5.20a and 5.20b, respectively.

## 5.5 Model evaluation

Testing the validity of both the basic and the extended model comprises comparison of observed leaf density and lamina density profiles with the profiles predicted by the two models. No records could be found in the literature in which both input and output variables of the models were determined independently. Therefore observations were made on an experimental perennial ryegrass - white clover sward on a sandy soil at Wageningen, The Netherlands (51°58' N latitude, 5°4' E longitude, 7 m altitude), as described by Nassiri (1998).

*5.5.1 Material and Methods*

The selected test plot was approximately 2 m x 2 m in size, and was located on a clay soil in Wageningen, The Netherlands. It had been cut 4 or 5 times yearly since it was sown in 1991, and received 150 kg $ha^{-1}$ of nitrogen yearly. Dressings of phosphorus and potassium had been supplied as required, based on soil tests. Measurements took place after a three week regrowth period, from the 23rd until the 25th August 2000. The sward was homogeneous and dominated by perennial ryegrass (*Lolium perenne*), cv. Barlet, and white clover (*Trifolium repens*), cvs. Gwenda and Alice. Generative tillers and clover inflorescents were absent.

**Direct observations**

The leaf density and lamina density profiles of both ryegrass and clover were measured directly using a 32.5° inclined point quadrat (Warren Wilson, 1963; see also Nassiri, 1998), which was moved into the sward at 140 random positions. In total, the contact heights with 327 grass leaves were recorded, of which 220 were contacts with grass lamina and 107 with grass sheaths. Similarly, 252 contact heights with white clover leaves were recorded, of which 164 were contacts with clover lamina and 88 with clover petioles. For both species, the total leaf area index and the total lamina density index was calculated as the average number of contacts per quadrat, multiplied by factors 1.13 and 1.16 for ryegrass and clover, respectively (Lantinga *et al.*, 1999).

**Indirect observations**

The required model input variables are given in the appendix. Of 250 grass leaves, the leaf top height and the sheath top height were measured. Of 253 clover leaves, the petiole top height was measured. To give equitable sampling probabilities to small and large leaves, all leaves of randomly chosen grass tillers and clover stolons were measured. After each observation, these tillers and stolons were carefully removed, and the leaf length and sheath length of all grass leaves, and the petiole length of all clover leaves were measured. Sixteen clover leaves with petiole lengths smaller than 1 cm were ignored, as it was obvious that these leaves had developed within the two days between the direct and the indirect measurements. Of each individual leaf, sheath and petiole, the ratio between the top height and the length was consequently calculated.

In order to obtain estimates for $\mu_{leaf}$, $\sigma_{leaf}$, $\mu_{sheath}$, $\sigma_{sheath}$, $\mu_{Tr\,pet}$ and $\sigma_{Tr\,pet}$, grass leaf lengths and sheath lengths, and clover leaf lengths were grouped into classes of 4 cms, and normal distributions were fitted (least summed squares method) to the observed frequency distributions. Differences between the observed and fitted frequencies were tested using the $\chi^2$ test, grouping classes with expected frequencies lower than 5 (Owen & Jones, 1990).

To derive estimates for $m_{leaf}$, $s_{leaf}$, $m_{sheath}$, $s_{sheath}$, $m_{Tr\,pet}$ and $s_{Tr\,pet}$, the ratios between the top heights and the lengths of grass leaves and sheaths, were grouped into classes of 0.1 width. The

ratios of clover petioles were grouped into classes of 0.2 width. Normal distributions "with denominator" (equation 5.12) were fitted to the observed frequency distributions, using the least summed squares method. Differences between observed and fitted frequencies were again tested using the $\chi^2$ test, grouping classes with expected frequencies lower than 5 (Owen & Jones, 1990).

The grass leaf and lamina density profiles of both grass and clover, as predicted by the basic and the extended models, were tested against the directly observed profiles using the $\chi^2$ test, grouping classes with predicted frequencies lower than 5 (Owen & Jones, 1990).

*5.5.2 Results*

The indirect measurements are illustrated in Figures 5.5 and 5.6, and the parameter values of the best fitting distributions are summarised in Table 5.1. For perennial ryegrass, the observed leaf length distribution differed significantly ($p < 0.05$) from the best fitting normal distribution (Figure 5.5a), indicating that the observed leaf lengths were in fact not normally distributed. The two maximums in the observed distribution reflect the two types of leaves which were present on the majority of tillers. The lower maximum was mainly made up of leaves which were expanding at the time of the last cutting event, whereas the upper maximum consisted largely of leaves which had developed after this event. Indeed most tillers only carried two or three leaves. In contrast, differences between the observed frequency distributions and the fitted normal distributions were insignificant ($p > 0.05$) for both grass sheath lengths and clover petiole lengths (Figures 5.5b and 5.5c).

Figure 5.6 and Table 5.1 show that entire grass leaves, grass sheaths, and clover petioles mainly had an erect orientation (high $m$). The height / length ratio of entire leaves showed a larger standard deviation than the ratio of sheaths only, which was caused by the more horizontal orientation of tall leaves, which were "bending over". For entire grass leaves and for grass sheaths, the observed frequency distributions of the height / length ratios differed significantly ($p < 0.05$) from the best fitting distributions, defined by equation 5.12. For clover petioles, this difference was insignificant ($p > 0.05$).

Figure 5.7 presents the density profiles of entire grass and clover leaves, as observed (shaded area) and as predicted by the basic model (single line) and by the extended model (bold line), and Figure 5.8 presents the density profiles of grass and clover lamina (note different scales of y-axes for each species). For both species, the lamina density and leaf density profiles as predicted by the extended model did not differ significantly ($p > 0.05$) from the directly observed profiles. Instead, the basic model significantly ($p < 0.001$) underestimated the areas of entire leaves and of lamina at the higher sward layers, and overestimated these at the bottom of the sward, for both species.

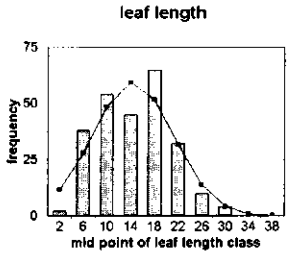


Figure 5.5a: Observed frequencies of leaf length classes, and best fitting normal distribution.

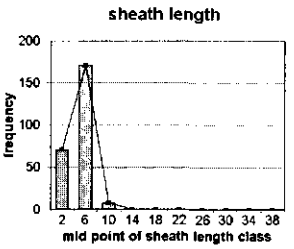


Figure 5.5b: Observed frequencies of sheath length classes, and best fitting normal distribution.

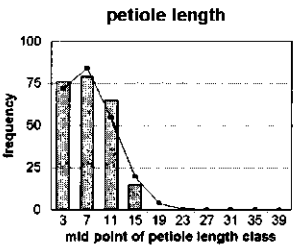


Figure 5.5c: Observed frequencies of petiole length classes, and best fitting normal distribution.

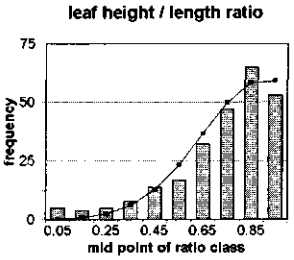


Figure 5.6a: Observed frequencies of leaf height / length ratio classes, and best fitting distribution (equation 5.12).

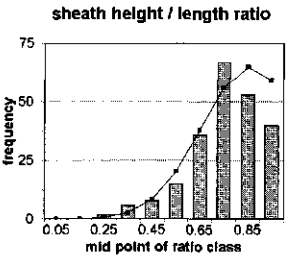


Figure 5.6b: Observed frequencies of sheath height / length ratio classes, and best fitting distribution (equation 5.12).

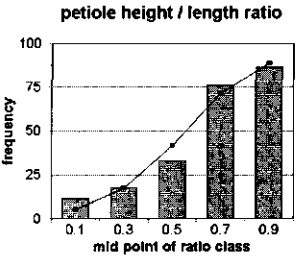


Figure 5.6c: Observed frequencies of petiole height / length ratio classes, and best fitting distribution (equation 5.12).

Table 5.1: Values of input variables of the basic and the extended model, based on the indirect observations.

| | value in distribution used by the models | | | | |
|---|---|---|---|---|---|
| variable | grass leaves | grass sheaths | clover petioles | clover lamina | used in |
| $\lambda$ (cm) | 14.7 | 4.9 | 7.18 | - | basic model |
| $\mu$ (cm) | 14.4 | 4.9 | 6.1 | - | extended model |
| $\sigma$ (cm) | 6.7 | 1.7 | 5.1 | - | extended model |
| $m$ (-) | 0.91 | 0.86 | 0.94 | - | extended model |
| $s$ (-) | 0.26 | 0.20 | 0.35 | - | extended model |
| $L_{tot}$ ($m^2$ $m^{-2}$) | 2.64 | 1.78 | 0.73 | 1.36 | both models |

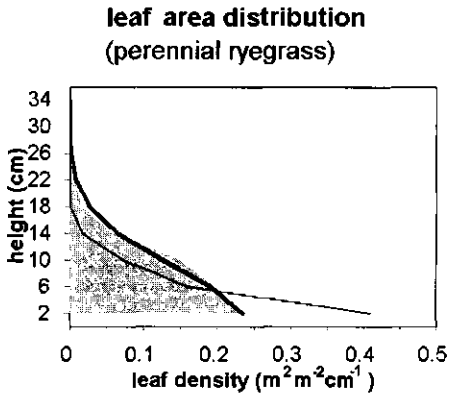


Figure 5.7a: Observed leaf density profile of perennial ryegrass (shaded area), and profiles predicted by the basic model (single line) and the extended model (bold line).

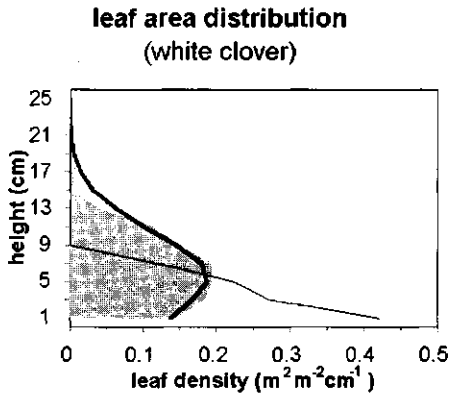


Figure 5.7b: Observed leaf density profile of white clover (shaded area), and profiles predicted by the basic model (single line) and the extended model (bold line).

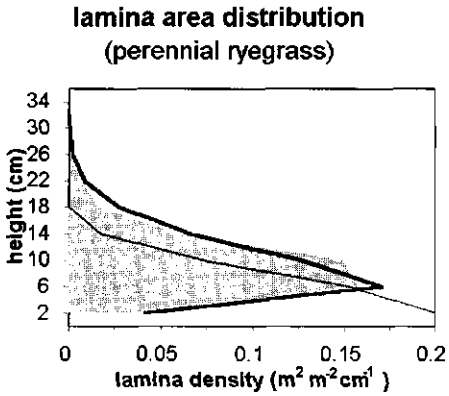


Figure 5.8a: Observed lamina density profile of perennial ryegrass (shaded area), and profiles predicted by the basic model (single line) and the extended model (bold line).

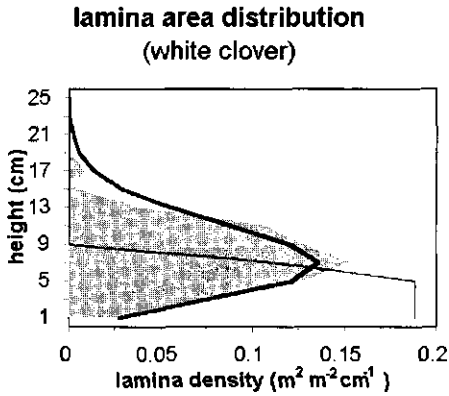


Figure 5.8b: Observed lamina density profile of white clover (shaded area), and profiles predicted by the basic model (single line) and the extended model (bold line).

## 5.6 Discussion

*5.6.1 Accuracy of the basic and the extended model*

The vertical leaf and lamina distributions of both perennial ryegrass and white clover were accurately simulated by the extended model. In contrast, the predictions of the basic model were largely inadequate. This difference in predictive capacities justifies the larger complexity of the extended model. As the basic model assumes that all leaves have equal lengths, it predicts the

absence of any leaf material at a height greater than the average leaf length. Using the double values of the average leaf length and sheath length for the basic model's input variables $\lambda_{leaf}$ and $\lambda_{sheath}$, respectively, improved the predictions of the basic model (not shown). However, changing these values did not change the shape of the predicted profiles, which clearly differs from the shapes of the observed profiles.

The extended model has shown a degree of robustness towards its initial assumptions: the profiles predicted by the extended model accurately matched those observed, in spite of the fact that the observed leaf and sheath lengths, and the observed top heights of each leaf and sheath length class were in fact not normally distributed, as assumed by the model. The validity of the third assumption of the extended model, i.e. the assumption of stiff and linear leaves (Figure 5.1a), was not tested directly. In fact leaves may only be assumed to be linear when leaves are small, as large leaves tend to "bend over" under their own weight (De Wit, 1965). Moreover, the spatial orientation of the sheath material and of the lamina material *within* individual grass leaves may not be identical (Gibson *et al.*, 1992), as was assumed in Figure 5.1a. In a further extension of the model, which is not presented here, leaves were described as arcs of a virtual circle. However, the small increase in accuracy which resulted from this extension did not justify the complex mathematics which were required.

*5.6.2 Flexibility of the extended model*

In the current experiment, both models were tested in a sward subjected to cutting regime. However, it was claimed above that there is a need for a model which is capable of accurately predicting the vertical structure of swards under a range of management systems. Therefore the flexibility of the extended model was explored by simulating sward profiles observed by Parsons *et al.* (1988). Using an inclined point quadrat, they presented the lamina density profiles of a perennial ryegrass sward at four stages during the summer: a) during continuous grazing at a grazing height of 5 cm, b) 14 days after release from continuous grazing, c) 14 days after a subsequent silage cut, and d) as the regrowing sward reached a ceiling yield. As these data only revealed the lamina density per cm height and the total lamina area $m^{-2}$, the remaining input variables of the extended model were either estimated or optimised, disqualifying this analysis from quantitative testing. The only aim is to demonstrate the flexibility of the extended model in simulating a wide range of qualitatively differing swards, and to show that the qualitative assumptions required to accurate simulation, as presented in Table 5.2, are realistic and predictable.

**Average leaf and sheath lengths**

Under continuous grazing at a sward height of 5 cm, most leaves were expected to be smaller than 5 cm. Therefore the average leaf length $\mu$ was estimated at 2.5 cm, which is the mean

Table 5.2: Assumed values of input variables of the extended model, required to simulate the sward structures observed by Parsons *et al.* (1988).

| | *assumed values* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | continuous grazing | | released | | regrowth | | ceiling yield | |
| variable | leaves | sheaths | leaves | sheaths | leaves | sheaths | leaves | sheaths |
| $\mu$ (cm) | 2.5 | 1.7 | 6.0 | 3.0 | 12.0 | 4.2 | 24.0 | 8.3 |
| $\sigma$ (cm) | 2.5 | 1.7 | 3.0 | 1.5 | 4.8 | 1.7 | 4.8 | 1.7 |
| $m$ (cm height $cm^{-1}$ length) | NA | NA | 0.75 | NA | 0.75 | 1.0 | 0.5 | 1.0 |
| $s$ (cm height $cm^{-1}$ length) | $\infty$ | $\infty$ | 0.5 | $\infty$ | 0.25 | 0.75 | 0.125 | 0.375 |
| (sheath / leaf length ratio) | (0.67) | | (0.5) | | (0.35) | | (0.35) | |

value of the largest leaves (5 cm) and new leaves (0 cm). Fourteen days after release from grazing, leaves were expected to have increased in length, and the average leaf length was optimised at 6 cm. As the sheath weight ratio of ungrazed, growing leaves is generally 0.35 (Parsons *et al.*, 1991a), yet the old leaves had been delaminated, the average sheath length was set at half the average leaf length (3 cm). Fourteen days after a subsequent silage cut, the average leaf length was optimised at 12 cm, which corresponds well with the average leaf length found in the current experiment, 21 days after cutting. The sheath weight ratio was now assumed to equal 0.35, leading to an average sheath length of 4.2 cm. Reaching a ceiling yield, both leaf and sheath lengths were assumed to have doubled to 24 cm and 8.3 cm, respectively. This average leaf length agrees with the assumption that in this growth stage, each ryegrass tiller would carry three leaves with a maximum leaf length of 30 cm (Sibma & Ennik, 1988; Van Loo, 1993), and one growing leaf with a length of half this value.

**Standard deviations of leaf and sheath lengths**

Due to continuous defoliation, the standard deviation of leaf and sheath lengths $\sigma$ was expected to be large under continuous grazing, and was set equal to the leaf and sheath lengths, at 2.5 and 1.7 cm, respectively. It was assumed that after release from grazing, the absence of defoliation reduced this variation of lengths, and the standard deviation of leaf and sheath lengths was set at half the average leaf and sheath lengths, as 3 and 1.5 cm, respectively. Regrowing from a silage cut, when defoliated leaves had been removed, the standard deviations were expected to have been reduced relatively, to 40% of the average leaf and sheath lengths, at 4.8 and 1.7,

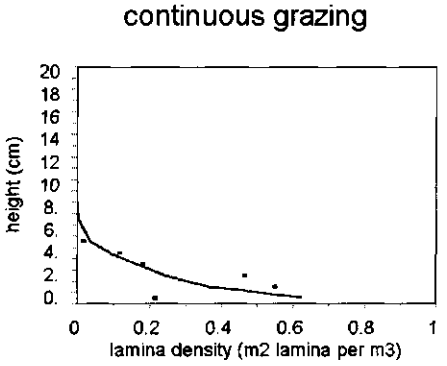


Figure 5.9a: Observed (squares) and predicted (line) lamina density profiles of a sward continuously grazed by sheep at 5 cm.

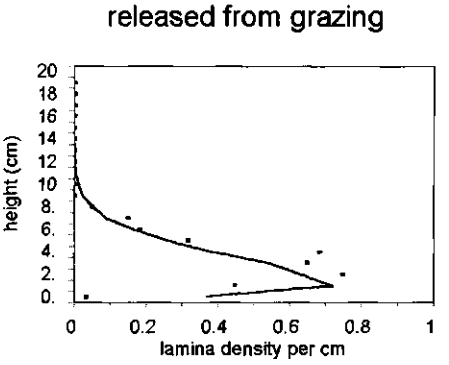


Figure 5.9b: Observed (squares) and predicted (line) lamina density profiles of the same sward, 14 days after the end of grazing.

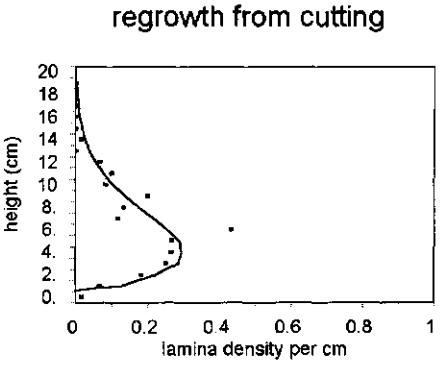


Figure 5.9c: Observed (squares) and predicted (line) lamina density profiles of the same sward, 14 days after a subsequent cut.

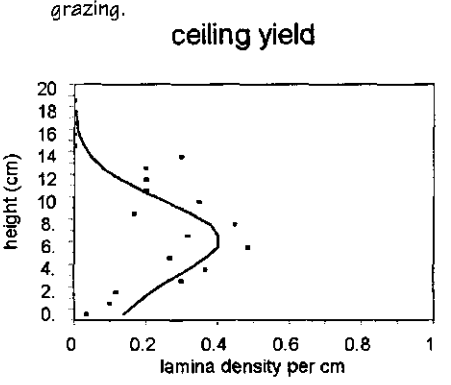


Figure 5.9d: Observed (squares) and predicted (line) lamina density profiles as the same sward reaches a ceiling yield.

respectively, which closely matches the values observed in the current experiment. Finally, as the sward reached a ceiling yield and each tiller may be assumed to carry three fully expanded leaves and one growing leaf of half the maximum length, the standard deviations of leaf and sheath lengths will have approached values approximately 20% of the lengths, resulting again in 4.8 and 1.7 cm.

**Relative leaf and sheath top heights and standard deviations**

Defoliation and treading by the animals was expected to have randomised the orientation of both leaves and sheaths under grazing, leading to uniform leaf top height and sheath top height distributions for each leaf and sheath length class. These uniform distributions can be simulated by setting the standard deviations of the relative leaf and sheath top heights in equation 5.12 to infinitive values ($s_{leaf} = s_{sheath} = \infty$), and the mean relative leaf and sheath top heights to any value between 0 and 1 ($m_{leaf} = m_{sheath}$ = N.A.). Fourteen days after release from grazing, entire leaves were

expected to have a rather erect orientation (see also De Wit, 1965) The relative leaf top height $m$ was set at 0.75, with a large standard deviation $s$, which was optimised at 0.5. The stiffer sheaths were expected to have responded more slowly to the absence of grazing, and still to show a random orientation. Fourteen days after the subsequent silage cut leaves were assumed to show the same average orientation, yet this time with a smaller standard deviation (0.25), as all grazed leaves had been removed. Sheaths were expected to show a more upright orientation, with an average relative sheath top height of 1. However, a considerable standard deviation of 0.75 was expected, due to the after-effects of treading. As the sward reached a ceiling yield, lodging was expected to have lead to a more horizontal orientation of leaves (see also De Wit, 1965), with an average relative leaf top height of 0.5. As this lodging would move leaf tops closer together, the standard deviation was halved to 0.125. The average relative sheath top height remained unchanged at 1. However, the standard deviation was halved to 0.375, as the after-effects of treading were expected to have weakened.

Figures 5.9a - 5.9d present the profiles observed by Parsons *et al.* (1988) (squares), and the profiles predicted by the extended model, based on the assumptions above. Apart from the close match between the observed and predicted profiles, the flexibility of the extended model is striking, as it is capable of simulating profiles with a wide range of shapes, caused by a wide range of grassland managements.

*5.6.3 Applications*

The flexibility and the accuracy of the extended model makes it a good candidate to be incorporated into existing grassland simulation models (e.g. Thornley, 1998), as a dynamic submodel. Replacing the static uniform, log-normal or triangular profiles which have been used to date, the extended model can aid the dynamic simulation of $CO_2$ assimilation and grazing patterns of swards of which the vertical structure changes over time, e.g. of swards under an alternating cutting and grazing regime.

Most of its input variables, i.e. the total grass leaf, lamina and sheath area and clover petiole, lamina, and leaf area, as well as the lengths of these components, can already be computed by existing models (e.g. Parsons *et al.*, 1991b; Van Loo, 1993; Thornley, 1998). Nevertheless, some of its required variables have not yet been produced by simulation to date. More and experimental research is required to reveal the relationship between the standard deviations of leaf and sheath lengths, and the spatial orientation of leaves on the one hand, and the grassland management practice on the other.

Some of these relationships were described by De Wit (1965), who found a largely erect orientation of leaves after a silage cut, and progressively more horizontal orientations during the

regrowth periods. Gibson *et al.* (1992) studied shoot and lamina angles of *Lolium multiflorum* and *Paspalum dilatatum* plants growing in various densities, in absence of grazing or cutting. They also found that shoot angles of both species decreased with time, which effect was progressively reduced with increasing plant densities. In contrast, lamina angles remained constant over time and between plant densities. Casey *et al.* (1999) studied the effect of the sheath tube length on the location and the depth of the elongation zone of perennial ryegrass leaves, which determined the leaf development. Their approach could serve as a starting point for the dynamic simulation of the mechanisms defining plant morphology.

Finally, application of the extended model to simulate the vertical profiles of grassland species other than perennial ryegrass and white clover, is easily envisaged. In fact perennial ryegrass could already be substituted by any grass species, in which vegetative tiller elongation is absent. Yet eventually even elongated tillers, both generative and vegetative, could be incorporated as a third plant component with a largely erect orientation.

Considering its accurate simulation of mixed vegetative sward, combined with the possibilities for further extensions, the extended model could not only be incorporated in existing grassland simulation models, but also serve the development of spatially explicit competition models.

## Acknowledgements

The authors are very grateful to Mr. Tony Hegarty, Teagasc HQ, for his critical review of the mathematics involved in this chapter, and to Drs. Jan Neuteboom, Wageningen University, for his patient help with the observations.

## Appendix Chapter 5

Input, internal, and output variables used in the basic and extended model

| | | | |
|---|---|---|---|
| Input variables | $\lambda_{leaf}$ , $\lambda_{sheath}$ , $\lambda_{Tr\ pet}$ | mean grass leaf, sheath and clover petiole length (basic model only) | m |
| | $W_{leaf\ tot}$ , $W_{sheath\ tot}$ , $W_{Tr\ pet\ tot}$ , $W_{Tr\ lam\ tot}$ | total grass leaf, sheath, and clover petiole, lamina weight | g $m^{-2}$ |
| | $L_{leaf\ tot}$ , $L_{sheath\ tot}$ , $L_{Tr\ pet\ tot}$ , $L_{Tr\ lam\ tot}$ | total grass leaf, sheath, and clover petiole, clover lamina area | $m^2$ $m^{-2}$ |
| | $\mu_{leaf}$ , $\mu_{sheath}$ , $\mu_{Tr\ pet}$ | mean grass leaf, sheath, and clover petiole length (extended model only) | m |
| | $\sigma_{leaf}$ , $\sigma_{sheath}$ , $\sigma_{Tr\ pet}$ | standard deviation of the grass leaf, sheath, and clover petiole length (extended model only) | m |
| | $m_{leaf}$ , $m_{sheath}$ , $m_{Tr\ pet}$ | mean grass leaf, sheath, and clover petiole top height, expressed as fraction of leaf, sheath, petiole length (extended model only) | - |
| | $s_{leaf}$ , $s_{sheath}$ , $s_{Tr\ pet}$ | standard deviation of the grass leaf, sheath, and clover petiole top height, expressed as fraction of leaf, sheath, petiole length (extended model only) | - |
| Internal variables | $h$ | measuring height, i.e. height under which the weights and areas are calculated | m |
| | $x$ | height of leaf, sheath, petiole top | m |
| | $f_h$ | fraction of an individual leaf, sheath, petiole, located under the measuring height $h$ | - |

| | | | |
|---|---|---|---|
| | $F(h)$ | fraction of all leaves, sheaths, petioles of a specific class, located under the measuring height $h$ (extended model only) | - |
| | $V(h)$ | fraction of all leaves, sheaths, petioles of all classes, that is located under the measuring height $h$. | - |
| | $\varphi(\lambda_{leaf})$, $\varphi(\lambda_{sheath})$, $\varphi(\lambda_{Tr\,pet})$ | frequency density distribution of leaf, sheath, petiole lengths (extended model only) | - |
| | $C(\lambda_{leaf})$, $C(\lambda_{sheath})$, $C(\lambda_{Tr\,pet})$ | relative contribution of each leaf, sheath, petiole length class to the weight or area of the total crop (extended model only) | - |
| | $p(x)$ | vertical probability density distribution of leaf, sheath, petiole tops. | number $m^{-2}$ $m^{-1}$ |
| Output variables | $W_{leaf\,1\text{-}2}$, $W_{sheath\,1\text{-}2}$, $W_{lam\,1\text{-}2}$, $W_{Tr\,pet\,1\text{-}2}$, $W_{Tr\,lam\,1\text{-}2}$, $W_{Tr\,leaf\,1\text{-}2}$ | Grass leaf, sheath, lamina weight and clover petiole, lamina and leaf weight in the sward layer between heights *h1* and *h2* | g $m^{-2}$ |
| | $L_{leaf\,1\text{-}2}$, $L_{sheath\,1\text{-}2}$, $L_{lam\,1\text{-}2}$, $L_{Tr\,pet\,1\text{-}2}$, $L_{Tr\,lam\,1\text{-}2}$, $L_{Tr\,leaf\,1\text{-}2}$ | Grass leaf, sheath, lamina area and clover petiole, lamina and leaf weight in sward layer between heights *h1* and *h2* | $m^2$ $m^{-2}$ |

# Chapter 6: Quantification of the lateral spatial heterogeneity of mixed pastures, using Dry Weight Rank data

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## Abstract

1) Mixtures of grasses and white clover may show fluctuating yields between years, caused by the delayed nitrogen transfer from white clover to the grass. As a result, phases of clover dominance and grass dominance alternate within patches of mixed grasslands. A stable production at field level may be achieved when individual patches fluctuate out of phase, compensating for each other's productivity. These compensating effects require a lateral heterogeneity of the sward.

2) In this chapter, a methodology is presented, based on the Dry Weight Rank method for botanical analysis of grasslands, which quantifies the lateral heterogeneity of mixed swards. Using this methodology, the impact of grassland management strategies on the heterogeneity of swards under sheep grazing is studied.

3) The heterogeneity of the total herbage mass and the heterogeneity of the white clover mass were affected in a dissimilar manner by the grassland management strategies. The heterogeneity of the total herbage mass was found to be highest after cutting, and under lenient grazing. Strip-grazing led to a homogeneous total herbage mass instead. The heterogeneity of the herbage mass of white clover showed the opposite response to management, as it was maximal under strip-grazing. The heterogeneities of the herbage masses of perennial ryegrass, creeping bentgrass and rough-stalked meadowgrass were not related to management parameters.

4) It is argued that the productivity and stability of mixed grasslands can only be understood by studying these at patch level. The methodology presented successfully quantified differences between individual patches. It is suggested that the impact of the grassland management on the spatial heterogeneity could be analysed even more conclusively by the use of quadrats with fixed locations.

## 6.1 Introduction

Recent years have seen a renewed interest in the use of white clover (*Trifolium repens*) in pastures, as a sustainable alternative to fertiliser nitrogen (Parsons *et al.*, 1991a,b; Laws & Newton, 1992; Schwinning & Parsons, 1996a). However, mixed pastures have frequently been associated with an unstable and hence unreliable herbage production (Curll *et al.*, 1985; Evans *et al.*, 1990; Orr *et al.*, 1990; Laws & Newton, 1992; Schwinning & Parsons, 1996a,b; Fothergill *et al.*, 2000). Poor clover performances have been related to *inter alia* the increased competitiveness of grasses under a nitrogen fertiliser regime (e.g. Curll, 1982; Curll *et al.*, 1985a,b; Silvertown & Dodd, 1994; Schwinning & Parsons, 1996a,b; Nassiri, 1998).

However, Thornley *et al.* (1995) and Schwinning & Parsons (1996a) showed that even in the absence of fertiliser nitrogen, mixtures of perennial ryegrass (*Lolium perenne*) and white clover may be intrinsically unstable, as had already been tentatively suggested by Parsons *et al.* (1991b). They related this intrinsic instability to the delayed nitrogen transfer from clover to ryegrass, which caused an oscillating herbage production of both clover and ryegrass between years (see also Chapter 2). Moreover, Thornley's (1998) simulation model of a grass monoculture also produced biannual yield oscillations, which were related to interactions between plants and the soil water status.

However, Schwinning & Parsons (1996b) argued that it depends on the spatial heterogeneity of mixed grasslands, whether these oscillations at a *patch* scale are also expressed at a *field* scale. Using a spatially explicit simulation model of a mixture of perennial ryegrass and white clover, they found that under grazing, the oscillations of individual patches were set "out of phase" by local tissue removal, and by urine and dung depositions (see also Chapter 2). Therefore, grazing increased the spatial heterogeneity of the mixture. Individual patches were found to compensate for each other, leading to a stable herbage production between years at field scale. In Chapter 2 it was suggested that the cutting of herbage would instead lead to spatially homogeneous grasslands, as this could synchronise the production oscillations of individual patches. As the yields of all patches would oscillate "in phase" under a cutting regime, fluctuations at patch scale would be sustained at field scale. These predictions were confirmed in Chapter 4, in which a high production stability was found of experimental pastures which were grazed by cattle, and a low production stability of swards under a continuous cutting regime, for all fertiliser regimes.

Although the urine and manure depositions under grazing lead to spatial heterogeneity, it is conceivable that this heterogeneity is simultaneously counteracted in case animals graze selectively

between patches. Especially sheep have a strong preference for clover, and declining clover contents have frequently been related to the ability of these animals to select for plant species (e.g. Milne *et al.*, 1982; Grant *et al.*, 1985; Binnie & Chestnutt, 1994). The impact of the grazing management on selective grazing and hence on the heterogeneity of pastures is uncertain. In Chapter, 2 it was noted that strip-grazing may lead to a uniform tissue removal among neighbouring patches. On the other hand, however, long grazing periods may lead to a continuous and uniform removal of tissue of the preferred species across the field (see also Laws & Newton, 1992). The relations between selective grazing, clover performance, and lateral heterogeneity were further explored by Parsons *et al.* (1994), also using a spatial simulation model. They predicted that the selectivity of animals may be reduced to a level of indifference when the fractional cover of the preferred species declines to low values, i.e. when the "searching time" for the preferred species limits the total daily intake rate.

Consequently, the production stability of mixed grasslands depends on their spatial heterogeneity. This spatial heterogeneity may be reduced by herbage cutting, and may be increased by faeces and urine deposition under grazing. At the same time, this heterogeneity under grazing may be counteracted by the effects of selective grazing between patches and between species by the animals.

In this chapter an attempt is made to identify and quantify the impact of the grassland management on the degree of spatial heterogeneity in mixed grasslands. Such an analysis requires an adequate quantification of the spatial heterogeneity. Neuteboom *et al.* (1992) used point-plant distances to characterise the lateral distribution of grassland plants. They compared observed distributions of point-plant distances with distribution which would theoretically arise under a random (Poisson) and aggregated (negative binomial) distribution of plants. However, it arguably is the spatial heterogeneity of the herbage mass rather than the heterogeneity of plant numbers that determine both the degree of selective grazing (e.g. Parsons *et al.*, 1994) and the mutual competition between plant species (e.g. Lantinga *et al.*, 1999; see also Chapter 5). For instance, a random distribution of plants across a field may result in a heterogeneous herbage mass, when individual plants differ in size, or in mixtures of species of different productivity.

Therefore, in this chapter a methodology is presented for the quantification of the spatial heterogeneity of the herbage masses of plant species in mixtures. Using this methodology, the effects of the grassland management on the spatial heterogeneity are studied.

## 6.2 Materials and Methods

*6.2.1 Experimental lay-out*

The case study in this chapter involves a field experiment at the experimental organic farm of Johnstown Castle Research Centre, in the South-East of Ireland. In spring 2000, 18 paddocks were laid out on a field which had been reseeded with perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in 1996. During the four years since reseeding, the entire site had been invaded by creeping bentgrass (*Agrostis stolonifera*), and by some minor weed species, of which rough-stalked meadowgrass (*Poa trivialis*) was most prominent.

The paddocks were divided into 2 replications consisting of 9 paddocks each, which differed in size from 0.014 to 0.133 ha. In early April 2000, the herbage of all paddocks was removed, and from 3rd May, both replications were rotationally grazed by two flocks of seven dry ewes (Suffolk and Texel). Each paddock was grazed until a residual sward height of 5 cm was reached. The average time required to reach this residual sward height ranged from 1 day on the smallest paddocks ("strip-grazing") to approximately 8 days on the largest paddocks ("lenient grazing"). On average, paddocks were grazed with intervals of approximately 30 days. During the month of June, each paddock was topped at 5 cm, immediately after grazing, in order to remove generative grass tillers.

The effects of strip-grazing vs. lenient grazing on the agronomic performance of the grass-clover swards are beyond the scope of the present study and will be reported on in a future publication (De Wolf & Schulte, *in prep.*).

*6.2.2 Observation methodology*

The day before each grazing, the botanical composition of each paddock was monitored using the Dry Weight Rank method for botanical composition (DWR) ('t Mannetje & Haydock, 1963), with yield correction (Jones & Hargreaves, 1979; Neuteboom *et al.*, 1998). This method was developed for a rapid analysis of the botanical composition in heterogeneous swards. A small sampling quadrat (3 $dm^2$) was placed on 40 locations in the sward. In each quadrat, a visual estimation was made which of the species took first, second and third rank, based on their contribution to the total herbage dry matter within the quadrat. The species which were ranked first, second or third, were allocated with fractions of 0.702, 0.211, and 0.087 respectively, of the total herbage mass within the quadrat. Finally, for each species the average of these fractional masses, relative to the average of the total mass of all quadrats, represented its estimated contribution to the total dry matter herbage mass in the paddock.

The total herbage mass within each quadrat was calculated from the height of the herbage within the quadrat, which was measured using a plate meter with a plate of 430 g, and 10 $dm^2$. The

correlation between the herbage height and the dry matter herbage mass was derived by measuring the heights of a total of 69 strips of 0.47 $m^2$, distributed over all paddocks, at various dates. These strips were consequently cut at a mowing height of c.4.5 cm. The herbage removed was dried overnight in a 100 °C oven, and weighed. Linear regression showed a strong correlation ($R^2 = 0.89$, $p < 0.001$) between the herbage height and the herbage dry matter weight.

In fact the DWR assumes that within each quadrat, *on average* the dominant species accounts for 70.2% of the local total herbage mass, the sub-dominant species for 21.1%, and the third species for 8.7%. For the calculation of the botanical composition, the inaccuracies arising from these crude assumptions per quadrat are compensated for by the large number of observations which can be made within a brief time period, which ensures that the spatial heterogeneity of swards is taken into account. Hence particularly in heterogeneous swards, in which species grow in patches, the DWR can prove more valuable than the cutting and hand-separating of a small number of samples ('t Mannetje & Haydock, 1963; Neuteboom *et al.*, 1998).

*6.2.3 Data analysis*

**Spatial heterogeneity of the total herbage mass**

The current case-study uses the DWR data of nine paddocks which had been grazed four times, i.e. in May, June, July and August, and the data of the nine remaining paddocks which had been grazed three times at the time of writing, i.e. in May, June, and July.

For each of the 40 quadrats within each paddock during each measurement, the local herbage mass was calculated as: herbage mass (g $m^{-2}$) = 29.9 × height (cm) - 134.6 . The spatial heterogeneity of the herbage mass, $\eta_{tot}$ was consequently quantified as the standard deviation of the local herbage mass, $s_{tot}$ (g $m^{-2}$), relative to the mean herbage mass of the paddock, $m_{tot}$ (g $m^{-2}$) (equation 6.1):

$$\eta_{tot} = \frac{s_{tot}}{m_{tot}} \qquad \text{Eq. 6.1}$$

$\eta_{tot}$ has no dimensions and is hence independent of the units in which the herbage mass is expressed (e.g. g $m^{-2}$ or kg $ha^{-1}$ ). More important, assuming a linear relationship between the herbage mass and its standard deviation (i.e. in absence of interactions), $\eta_{tot}$ is independent of the average herbage mass on the paddock at the time of observations. This independence consequently allowed a mutual comparison of the heterogeneity of paddocks with different herbage masses at the time of measuring.

**Spatial heterogeneity of the herbage mass of individual species**

It was assumed that within each quadrat, the species ranked first, second, and third, each accounted for exactly 70.2%, 21.1%, and 8.7% of the local herbage mass, respectively. The real fractions they accounted for are unknown, and may differ from these average fractions. Neuteboom *et al.* (1998) studied the accuracy of the DWR and its assumptions by means of simulation. They indicated that within individual quadrats, the species ranked first, second and third may account for herbage fractions which are different from the average fractions of 0.702, 0.211 and 0.087. However, they showed that the largest discrepancies appeared in homogeneous swards, when large quadrats (8.7 $dm^2$) were used. When using smaller quadrats in heterogeneous swards instead, the fractional contributions of the species ranked first, second and third, were close to the average fractions of 0.702, 0.211 and 0.087, although some deviations were still observed, in particular for the dominant species.However, the large number of observations per paddock (40 quadrats x 3 ranks) in the present study may be expected to result in equal probabilities of overestimations and underestimations. Noteworthily, other values for the fractions accounted for by the species ranked first, second, and third, have also been reported (e.g. Jones & Hargreaves, 1979).

The heterogeneity of the estimated herbage mass of each individual species, $\eta_i$, was calculated similarly to the heterogeneity of the total herbage mass (equation 6.2):

$$\eta_i = \frac{s_i}{m_i} \qquad \text{Eq. 6.2}$$

in which the suffix *i* is replaced by *Lp*, *Tr*, *As*, or *Pt*, to indicate perennial ryegrass, white clover, creeping bentgrass, and rough-stalked meadowgrass, respectively. Here, $s_i$ and $m_i$ indicate the standard deviation and the average herbage mass of species *i*, in quadrats *in which it was present*. This means that "zero-observations", i.e. quadrats in which species *i* was absent, were excluded from the calculation of $\eta_i$. This ensures that $\eta_i$ is does not depend on the presence frequency of the species in each individual paddock. Similar to $\eta_{tot}$ , the heterogeneity of individual species is also independent of the units in which the herbage mass is expressed, as well as independent of the total herbage yield of the paddock.

The heterogeneity of herbage mass of each species was only calculated for paddocks in which the species was observed in at least 10 quadrats.

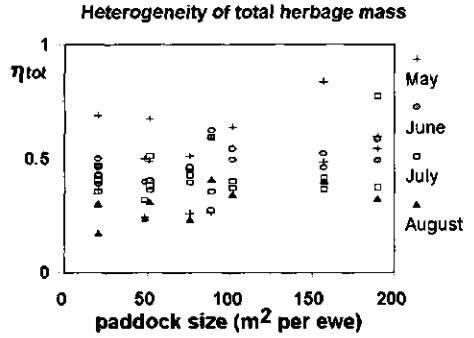


Figure 6.1: The effects of paddock size and time on the spatial heterogeneity of the total herbage mass. Results of 17 assessments in each of the months of May, June and July, and 9 paddocks in August.

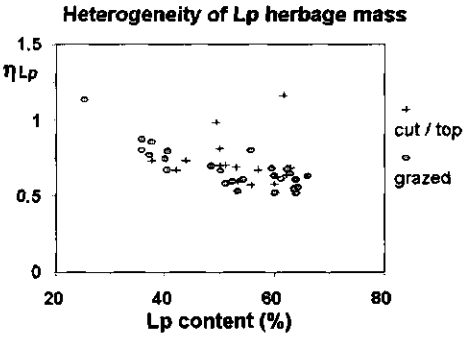


Figure 6.2: The effects of the ryegrass content in the swards and of management on the spatial heterogeneity of the ryegrass herbage mass. Results of 34 assessments after cutting or topping, and 26 after grazing.

## 6.3 Results

### *6.3.1 Heterogeneity of the total herbage mass*

Multiple linear regression was used to explain the heterogeneity of the total herbage mass by the paddock size and by the number of months elapsed since the start of the experiment, i.e. from zero in May up to three in August. On all plots, the spatial heterogeneity of the total herbage mass was significantly reduced over time ($p < 0.001$). Figure 6.1 shows that the reduction of the heterogeneity was additionally inversely related to the paddock size ($p < 0.025$). Therefore strip-grazing (small paddocks) led to a progressively more homogeneous herbage mass than lenient grazing.

### *6.3.2 Heterogeneity of the herbage masses of individual species*

**Perennial ryegrass**

No correlation was observed between the heterogeneity of the herbage mass of perennial ryegrass and either the paddock size or time. However, a significant negative correlation ($p < 0.025$) was found between $\eta_{Lp}$ and the content of perennial ryegrass in the sward of each paddock. This implies that the heterogeneity of perennial ryegrass was lower in absence of interactions with other species. Figure 6.2 shows that this negative relation was most prominent when measured after grazing (i.e. in June and August), whereas this relationship was absent when measured after a cutting or topping event (i.e. in May and July). For the combined observations of June and August, the correlation between $\eta_{Lp}$ and the ryegrass content was most significant ($p < 0.001$). For these

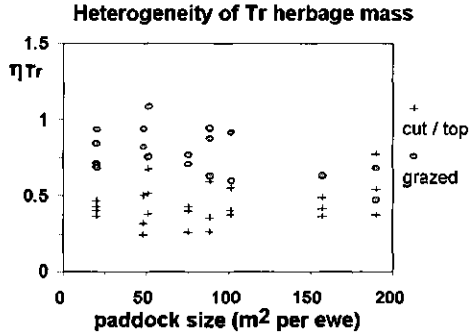


Figure 6.3: The effects of paddock size and management on the spatial heterogeneity of the clover herbage mass. Results of 27 measurements after cutting or topping, and 29 after grazing, in paddocks in which $PF_{Tr} \geq 0.25$.

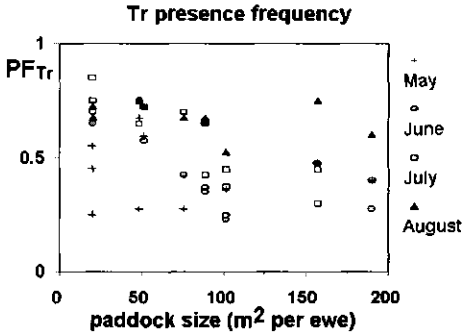


Figure 6.4: The effects of paddock size and time on the presence frequency of white clover. Results of 11 measurements in May, 12 in June, 15 in July, and 9 in August, in paddocks in which $PF_{Tr} \geq 0.25$.

months, neither $\eta_{Lp}$ nor the ryegrass content were correlated to either the paddock size or the month of observation. Therefore the dependence observed here, of $\eta_{Lp}$ on the ryegrass content, is not the result of indirect relations. Linear extrapolation of $\eta_{Lp}$ revealed a heterogeneity as low as 0.22 for a grazed ryegrass monoculture (Lp content = 100%) after grazing. This implies that the herbage mass of ryegrass monocultures would be more homogeneous than the herbage mass of the mixtures observed above.

**White clover**

Multiple regression revealed no significant correlation between the heterogeneity of the white clover mass and the month of observation. However, the $\eta_{Tr}$ was significantly higher ($p < 0.001$) when observed after grazing (June, August) than after cutting or topping (May, July). Moreover, after grazing $\eta_{Tr}$ did depend significantly ($p < 0.025$) on the paddock size. Figure 6.3 shows that after grazing, a larger heterogeneity of the clover herbage mass was observed under strip-grazing (small paddocks) than under lenient grazing (large paddocks). Observations made after cutting or topping did not show this relationship.

Before the commencement of grazing in May, the presence frequency of white clover, $PF_{Tr}$, i.e. the fractional number of quadrats in which clover was present, was not related to the paddock size. Contrastingly, $PF_{Tr}$ was strongly related ($p < 0.001$) to the paddock size, after the start of grazing (i.e. all data excluding May). Additionally, the interaction between paddock size and the month was also found to have a significant effect ($p < 0.01$) on $PF_{Tr}$. This means that strip-grazing led to an increasing presence frequency of white clover, whereas this frequency declined under lenient grazing. However, this effect was progressively reduced during July and August. This is illustrated in Figure 6.4.

**Creeping bentgrass**

No correlations between the spatial heterogeneity of the herbage mass of creeping bentgrass and the paddock size were found, neither for observations made after grazing, nor after cutting or topping. Neither could $\eta_{As}$ be related to the bentgrass content in the sward or the month of observation.

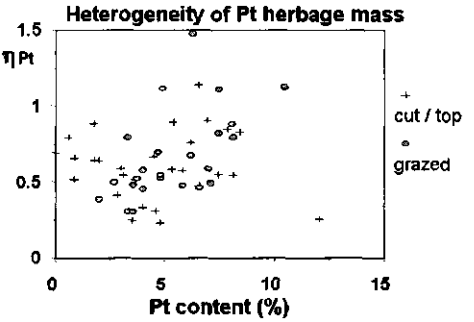


*Figure 6.5: The effects of the meadowgrass content in the swards and of management on the spatial heterogeneity of the meadowgrass herbage mass. Results of 29 measurements after cutting or topping, and 24 after grazing in paddocks in which $PF_{Pt} \geq 0.25$.*

**Rough-stalked meadowgrass**

The heterogeneity of the herbage mass of rough-stalked meadowgrass did not depend on the paddock size, neither for observations made after grazing, nor after cutting or topping. However, after grazing $\eta_{Pt}$ was significantly related ($p < 0.01$) to the meadowgrass content of the sward (Figure 6.5). Similar to perennial ryegrass, $\eta_{Pt}$ nor the meadowgrass content of the sward were related to either the paddock size or the month of observation. Therefore the relation between $\eta_{Pt}$ and the meadowgrass content was not an indirect relationship. Surprisingly, $\eta_{Pt}$, was higher for swards containing a larger proportion of meadowgrass. This means that the heterogeneity of meadowgrass was reduced by interactions with the other plant species. Extrapolation of $\eta_{Pt}$ to a monoculture of rough-stalked meadowgrass was not performed, however, as the meadowgrass content in the sward never exceeded 15%.

## 6.4 Discussion

The various aspects of grassland management which were imposed on the paddocks, led to a wide range of spatial responses of the plant species in the sward. The responses of individual plant species, in particularly that of white clover, differed both quantitatively and qualitatively from the response of the total herbage mass.

The heterogeneity of the total herbage mass declined during the experiment (Figure 6.1). In fact this heterogeneity was highest when measured after a cutting event (May), and progressively lower after each grazing, in spite of the urine and manure depositions, which were expected to have increased the heterogeneity.

Additionally, strip-grazing led to a stronger decrease of spatial heterogeneity than lenient grazing (Figure 6.1), even though the density of urine patches (patches $m^{-2}$) was identical on all

paddocks. The stronger increase under strip-grazing is in line with the notion in Chapter 2 that strip-grazing would synchronise the developmental phases of all patches in a paddock. Under strip-grazing, all plants on all patches were reduced to their stubble layer within one day, after which regrowth could recommence. Contrastingly, under lenient grazing periods of defoliation and regrowth alternated on individual patches for at least 8 days. By the end of the grazing period, patches may have differed in their developmental stages as a result.

The heterogeneity of the white clover herbage mass showed the opposite response to management. An increase was observed after grazing, except when paddocks were topped after the second grazing (July) (Figure 6.3). It is conceivable that the manure and urine depositions had a stronger effect on the clover performance, than on the total herbage mass. The sensitivity of clover to urine and manure agrees with the declining clover performance under nitrogen applications, when in competition with grasses (Curll, 1982; Curll *et al.*, 1985a,b; Silvertown & Dodd, 1994; Schwinning & Parsons, 1996a,b; Nassiri, 1998). The lower sensitivity of the total herbage mass to urine and manure can then be understood by considering the niche-differentiation of grasses and white clover in response to the soil nitrogen status. The performance of perennial ryegrass is generally enhanced on urine patches, whilst white clover prefers patches depleted of nitrogen (Schwinning & Parsons, 1996a,b; Chapter 2; see also Silvertown, 1980). Therefore ryegrass and clover may have compensated for each other on different patches, thereby eliminating the effects of urine and manure depositions on the spatial heterogeneity of the total herbage mass.

The spatial heterogeneity of the white clover mass increased strongest on the smallest paddocks, whereas no increase was observed under lenient grazing (Figure 6.3). This is in line with the hypothesis of Chapter 2, which stated that under strip-grazing, the animals can only exploit their preference for clover for a very short period, after which only grasses remained on offer. Under lenient grazing, the longer residence time of animals in a paddock allows the animals to select for regrowing clover tissue, leading to a uniform clover depletion across the field (Chapter 2; De Wolf & Schulte, *in prep.*; see also Laws & Newton, 1992).

This uniform depletion was confirmed by the lower presence frequency of white clover on the larger paddocks (Figure 6.4). However, the effects of this depletion were reduced over time. In August, the clover presence frequency was only slightly lower on the larger paddocks than on the smaller ones. This could either result from the seasonal growth pattern of white clover (Frame, 1990), or from the plasticity of white clover with respect to its leaf size. During the experiment, progressively smaller clover leaves were visually observed under lenient grazing. This "escape mechanism" from grazing (Noy-Meir, 1975; Chapter 2) may progressively have counteracted the effects of the strong selective grazing under lenient grazing.

The spatial heterogeneity of either of the other individual plant species, i.e. perennial ryegrass, creeping bentgrass, and rough-stalked meadowgrass, was not related to any management aspects, or to time. However, the heterogeneity of perennial ryegrass was negatively related to its content in the sward, especially under grazing (Figure 6.2). Conversely, the heterogeneity of rough-stalked bentgrass was positively correlated to its content in the sward under grazing (Figure 6.5).

In summary, the heterogeneity of the total herbage mass was maximal under cutting and under lenient grazing, whereas the heterogeneity of the clover herbage mass was highest under strip-grazing. More experimental data, measured during several grazing seasons, are required to reveal the cause of this discrepancy more conclusively. In the current experiment, the locations of the quadrats were randomly chosen during each assessment. The response of plants species to management parameters could be determined more accurately by using fixed quadrats, instead.

Additionally, it should be kept in mind, that the observed responses of the heterogeneities to the management may be limited to the current experiment. Different responses may be expected in a different ecosystem or in a different environment. For instance, grazing characteristics dissimilar to those of the dry ewes used in the current experiment, have been observed with cattle (e.g. Milne *et al.*, 1982), and even with lactating ewes (e.g. Penning *et al.*, 1995). Also, diverging plant responses to the nitrogen in urine and different degrees of niche-differentiation between plants may be expected in mixtures of other grassland species, as well as under other soil conditions (Silvertown, 1980, see also Chapters 2 and 4).

The conflicting effects of the grassland management on the heterogeneity of the total herbage mass on the one hand, and the heterogeneity of the herbage mass of white clover on the other, raises the question which management strategy would lead to a maximum stability of grass-clover mixtures at field scale. Schwinning & Parsons (1996a,b) related the fluctuating production of patches in absence of fertiliser nitrogen to the delayed nitrogen transfer from clover to grasses. They predicted that this delay would lead to alternating periods of grass dominance and clover dominance in each patch (see also Chapter 2). Indeed, in Chapter 4, large yield oscillations of experimental plots were found under a cutting regime in absence of nitrogen fertiliser. Consequently, patches may compensate for each other when they differ in clover content, which could be achieved by subjecting the pasture to strip-grazing.

In Chapter 2 it was argued that the effects of the management on the production stability of mixed grasslands is mediated at least partly by the lateral heterogeneity of the latter. In this light it is surprising how the lateral spatial dimensions are commonly ignored in grassland studies, both experimental and theoretical, with only few exceptions (e.g. Chapman, 1983; Parsons *et al.*, 1994;

Schwinning & Parsons, 1996b; Brereton & McGilloway, 1999). In most studies, paddocks are considered as one uniform and "average" patch, instead. The methodology presented in this chapter was successfully applied to field data, in order to quantify the lateral heterogeneity of mixed grassland, and its dependence on the grassland management. Using this methodology, the heterogeneity of the total herbage mass and the heterogeneity of the clover mass were found to be affected rapidly and significantly by the managements imposed.

However, the restrictions of this methodology should be appreciated. Firstly, it was assumed that the species ranked first, second and third in each quadrat, always accounted for 70.2%, 20.1, and 8.7% of the dry matter weight within the quadrat. The inaccuracies arising from this assumption may lead to a systematic increase of $\eta_i$, i.e. of the standard deviation of the herbage mass of each species. Secondly, using the Dry Weight Rank method for botanical assessment, only the three most dominant species are scored within each quadrats. As a result, species are not being recorded in quadrats in which they grow in very low densities. This failure to record low densities may lead to a systematic decrease of $\eta_i$, instead.

Nevertheless, the methodology presented is of low complexity, and can be applied to existing databases of Dry Weight Rank measurements. Therefore it could aid the analysis of the relations between grassland management strategies on the one hand, and the spatial heterogeneity mixed pastures on the other. When grasslands are assessed during a large number of years, using quadrats with fixed locations, it is conceivable that the methodology presented in this chapter could eventually reveal the impact of grazing management strategies on the production stability of mixed grasslands.

**Acknowledgements**

The authors are very grateful to Mr. Pieter de Wolf, for the management of the experiment, and for his patient collection of the large amounts of data used in this study.

# Chapter 7: Advanced analysis of Dry Weight Rank data to discriminate direct and indirect interactions between white clover and grasses in a multi-species pasture under a range of management strategies.

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## Abstract

1) Interactions between white clover and perennial ryegrass have been well documented. However, the interactions between white clover and weed species are less well understood. Particularly the invasions of pastures by creeping bentgrass may compromise clover performance.

2) Strategies to prevent creeping bentgrass infestations require an understanding of its interactions with white clover, as the exclusion of white clover from infested pastures could be the result of either direct competition or niche-differentiation in response to management.

3) A methodology is presented which enables the segregation of the effects of direct competition and niche-differentiation, based on existing Dry Weight Rank measurements of a number of experimental pastures, subjected to a range of management strategies.

4) Only between the two management extremities, i.e. permanent silage cutting and lenient grazing for long periods, did niche-differentiation occur between white clover and creeping bentgrass. White clover performance was enhanced under the cutting regime, whereas the long grazing periods stimulated the growth of creeping bentgrass. No niche-differentiation occurred in response to any other management regime.

5) White clover was instead actively excluded from creeping-bentgrass dominated patches by direct competition, whereas it showed a high compatibility with perennial ryegrass.

6) This direct interaction presents challenges to the prevention of creeping bentgrass by management, as creeping bentgrass and white clover showed nearly identical requirements in terms of environment and grassland management. A sequence of silage cuts may be the only tool to reduce bentgrass infestations.

## 7.1 Introduction

White clover (*Trifolium repens*) plays an increasingly important role in mixed pastures as a sustainable alternative to nitrogen fertiliser (Parsons *et al.*, 1991a,b; Laws & Newton, 1992; Schwinning & Parsons, 1996a). However, the maintenance of a high and stable clover content has presented considerable challenges to date (Curll *et al.*, 1985a,b; Evans *et al.*, 1990; Orr *et al.*, 1990; Laws & Newton, 1992; Schwinning & Parsons, 1996a,b; Fothergill *et al.*, 2000). Poor clover performances have frequently been related to increased competitiveness of grasses under a nitrogen fertiliser regime (e.g. Curll, 1982; Curll *et al.*, 1985a,b; Silvertown & Dodd, 1994; Schwinning & Parsons, 1996a,b; Nassiri, 1998). Alternatively, in absence of nitrogen fertiliser, declining clover contents have been attributed to selective grazing by animals (Curll *et al.*, 1985a,b; Parsons *et al.*, 1991b; Evans *et al.*, 1992; Parsons *et al.*, 1994, Fothergill *et al.*, 2000).

Most of these theoretical and experimental studies have focussed on the interactions between white clover and perennial ryegrass (*Lolium perenne*) only. The open and non-stoloniferous morphology of perennial ryegrass ensures a relatively high compatibility with white clover (Frame, 1990). In Ireland, where the current study was conducted, most seed mixtures which include white clover consequently consist of various ratios and varieties of perennial ryegrass and white clover only (Culleton & McGilloway, 1994). However, reseeded pastures are commonly invaded by weeds over time. Particularly the extensively managed pastures, on which artificial nitrogen and herbicide inputs are limited, are confronted with weed grasses. Creeping bentgrass (*Agrostis stolonifera*) is the most widespread weed in Ireland. It will be shown that locally, this stoloniferous grass can form dense patches, in which white clover is suppressed.

The prevention of this domination by creeping bentgrass requires an understanding of the negative interactions between creeping bentgrass and white clover, as these interactions may be either direct or indirect. Direct interactions entail the competition for light, space, and nutrients between adjacent plants of both species. Alternatively, indirect interactions involve the niche-differentiation between both species with respect to management, or soil and climatic conditions. In case these indirect interactions prevail, white clover and creeping bentgrass would not grow simultaneously in mixed swards because each species requires a partially different environment to grow (see also Silvertown, 1980).

This distinction between indirect niche-differentiation and direct competition has significant consequences for strategies to prevent creeping bentgrass infestations: in case the two species would be incompatible because they require partially different environments, creeping bentgrass would mainly be an indicator species, suggesting that the environment or the grassland management is not

optimal for white clover growth. In that case it is conceivable that a change of grassland management could prevent creeping bentgrass, while enhancing white clover performance. Conversely, if the exclusion of white clover is merely the result of direct competition, this would pose a more serious challenge, as it would imply that both species have identical requirements in terms of environment, resources and management. This would mean that grassland management strategies which enhance clover performance would simultaneously encourage creeping bentgrass infestations.

In this chapter a data analysis methodology is presented, which discriminates and quantifies these direct and indirect interactions between creeping bentgrass and white clover, under a wide range of grassland management strategies. This methodology is based on the Dry Weight Rank Method for botanical analysis of grasslands ('t Mannetje & Haydock, 1963). Therefore it can be applied to existing field data, i.e. to Dry Weight Rank data which have been collected in the past.

## 7.2 Materials and methods

*7.2.1 Experimental lay-out*

The case study in this chapter involves a field experiment at the experimental organic farm of Johnstown Castle Research Centre, in the South-East of Ireland. In the spring of 1998, 16 paddocks ranging in size from 0.014 to 0.133 ha, were laid out in a field which was selected for its homogeneity. This field had been reseeded with perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) two years previously, and which had received 25 tonnes $ha^{-1}$ of farm yard manure (cattle) in 1997. The field had been managed organically, which means that no artificial fertiliser nor any herbicides had been applied. During the two years following reseeding, the entire field had been invaded by creeping bentgrass (*Agrostis stolonifera*) and by some minor weed species, of which *Poa trivialis*, *Ranunculus repens*, and *Rumex obtusifolius* were present most frequently.

Five different grassland management systems were imposed on the paddocks, all of which involved grazing with cattle and sheep, and the conservation of silage. These management systems entailed a limited number of combinations of three management aspects:

a) "Hard" vs. "lenient" grazing, which means grazing at high or low instantaneous stocking rates (number of livestock units per area of the *paddock*).

b) The integration of silage cutting into the grazing rotation vs. the separation of silage and

grazing areas.

c) Mixed grazing of cattle and sheep on each paddock vs. separate paddocks for cattle and sheep.

The five subsequent grassland management systems were:

1) Lenient, integrated, and mixed grazing (2 paddocks): each field was grazed 3.75 weeks by cattle (yearlings), 3.75 weeks by lactating ewes, followed by a rest period of 4 weeks, a subsequent silage cut, and a regrowth period of 3.5 weeks. The order of grazing and cutting was reversed on the duplicate paddock.

2) Lenient, integrated, separate grazing (4 paddocks): each field was grazed for 7.5 weeks, either by lactating ewes or by cattle (yearlings), followed by a rest period of 4 weeks, a subsequent silage cut, and a regrowth period of 3.5 weeks. The order of grazing and cutting was reversed on the two duplicate paddocks.

3) Lenient, non-integrated, mixed grazing (4 paddocks): two thirds of the fields were grazed 3.75 weeks by cattle (yearlings) and 3.75 weeks by lactating ewes, followed by a rest period of 7.5 weeks. The order of grazing and the rest period was reversed on the duplicate paddock. The remaining third of the fields were cut for silage.

4) Hard, integrated, mixed grazing (2 paddocks): as system 1, but the grazing, rest, and regrowth periods were half the length.

5) Hard, non-integrated, separate grazing (4 paddocks): as system 3, but the grazing and rest periods were half the length.

Paddock sizes were adjusted in order to obtain an yearly average stocking rate of 1.5 livestock units $ha^{-1}$ for each management system.

*7.2.2 Observation methodology*

The botanical composition of each paddock was assessed using the Dry Weight Rank Method (DWR) ('t Mannetje & Haydock, 1963). This method was developed for a rapid analysis of the botanical composition in heterogeneous swards. A small sample quadrat is placed on a large number of locations in the sward. In each quadrat, the observer visually estimates the species which take first, second and third rank, based on their contribution to the total herbage dry matter within the quadrat. For each species, the percentages of quadrats in which it is ranked first, second or third, are multiplied by the values 0.702, 0.211, and 0.087, respectively. Finally, for each species the average of these products represents its estimated contribution to the total dry matter herbage mass. For further details on the DWR see 't Mannetje & Haydock (1963), Jones & Hargreaves (1979), and Neuteboom *et al.* (1998).

In fact the DWR assumes that within each quadrat, *on average* the dominant species

accounts for 70.2% of the local total herbage mass, the sub-dominant species for 21.1%, and the third species for 8.7%. The inaccuracies arising from these crude assumptions per quadrat are compensated for by the large number of observations which can be made within a brief time period, which ensures that the spatial heterogeneity of swards is taken into account. Hence particularly in heterogeneous swards, in which species grow in patches, the DWR can prove more valuable than the cutting and hand-separating of a small number of samples ('t Mannetje & Haydock, 1963; Neuteboom *et al.*, 1998).

In the current experiment, 30 quadrats of 3 $dm^2$ were used to assess the botanical composition of each paddock before each grazing period, rest period, or silage cut. These 30 quadrats per paddock, recorded during one observation period will be referred to as an "observation set". The relatively small number of quadrats within these observation sets was compensated for by the high sampling frequency (every three weeks on average). It will be shown that the observation sets of each paddock did not change significantly over time. As a result, all observation sets of each paddock could be treated as replications.

On all paddocks, during the entire experiment, either perennial ryegrass or creeping bentgrass were ranked as the dominant species in the vast majority of quadrats. Only on the paddocks which were cut for silage only, did white clover dominate approximately 9% of the quadrats during the observed time course. Most of the second and third ranks were allocated to either perennial ryegrass, creeping bentgrass, white clover or rough-stalked meadowgrass (*Poa trivialis*). The remaining grass species and forbs were usually ranked second or third, and only sporadically as first. For the purpose of readability, perennial ryegrass, creeping bentgrass, and white clover will generally be referred to as ryegrass, bentgrass, and clover, respectively.

*7.2.3 Data analysis*

The DWR is commonly used to record the botanical composition of pastures only. However, the listing of local combinations of dominant, sub-dominant, and third species conceals additional information on the nature of the mutual interactions between these species, by recording the distribution of species *between* paddocks as well as *within* paddocks.

Figure 7.1 illustrates four hypothetical scenario's of the distributions of ryegrass, bentgrass, and clover, which arise in case the species either do not interact (Figure 7.1a), show direct competition only (Figure 7.1b), show niche-differentiation only (Figure 7.1c), or show both direct competition and niche-differentiation (Figure 7.1d). Figure 7.1a shows that in absence of interactions between the species, the fraction of ryegrass dominated quadrats in which clover is present, equals the fraction of bentgrass dominated quadrats in which clover is present, i.e. 0.5 under both management regimes. In case bentgrass tends to exclude clover by direct competition (Figure 7.1b), clover is present in a smaller proportion of the bentgrass dominated quadrats (0.33 in Figure 7.1b),

than of ryegrass dominated patches (0.67 in Figure 7.1b). However, the three species remain equally distributed between the two management regimes. Contrastingly, when ryegrass, bentgrass and clover show niche-differentiation in response to the management regime, the species are distributed asymmetrically between the paddocks. In Figure 7.1c the ryegrass and clover performance has been enhanced by management A, whereas the growth of bentgrass has been stimulated by management B. Due to this asymmetric distribution, the number of bentgrass dominated quadrats in which clover is present has decreased from 6 in Figure 7.1a to 5 in Figure 7.1c. However, *within* each paddock, the fraction of bentgrass dominated quadrats in which clover is present, equals the fraction of ryegrass dominated quadrats in which clover is present (0.67 under management A, 0.33 under management B). Finally, when both direct and indirect interactions are present, the species are distributed asymmetrically both *between* and *within* paddocks.

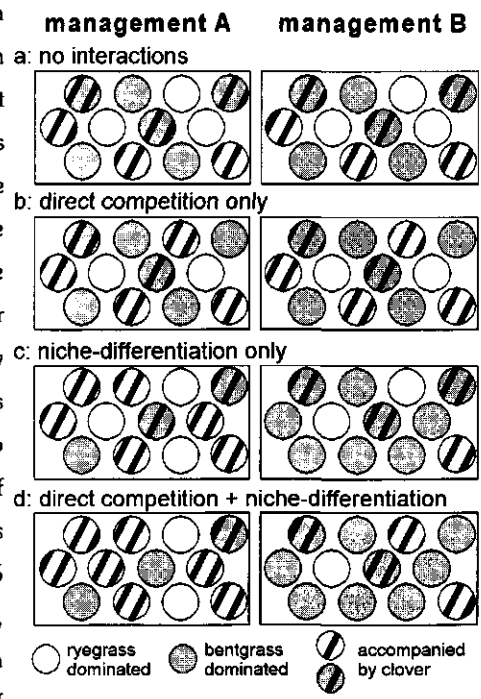


Figure 7.1: Four hypothetical scenario's, in which ryegrass, bentgrass and clover show no interactions, direct interactions only, indirect interactions only, or both direct and indirect interactions. In each scenario, half of the quadrats are dominated by ryegrass (white circles), and half by bentgrass (shaded circles). Clover is present in half of all quadrats (dashed circles).

Summarising, direct competition leads to an asymmetric distribution of clover over ryegrass and bentgrass dominated quadrats *within* paddocks. Contrastingly, niche-differentiation leads to an asymmetric distribution *between* paddocks.

The degree of the niche-differentiation and direct competition among the observed species can then be deducted by comparing the observed frequencies of species combinations with the frequencies which are expected when:

1) species are distributed equally within and between paddocks, i.e. when direct competition and niche-differentiation are absent.
2) species are distributed equally within paddocks and between paddocks under identical management regimes, but asymmetrically between paddocks under different management regimes, which arises when competition is absent, but species show niche-differentiation in response to management.

3) species are distributed equally within paddocks, but asymmetrically between all paddocks, which arises when direct competition is absent, but species show niche-differentiation in response to an unknown complex of factors.

It is assumed that each individual paddock forms a homogeneous niche for plants in terms of management, soil conditions, and time, i.e. environmental and management conditions of all quadrats *within* each paddock are identical.

**Expected frequencies in absence of interactions**

In the event that ryegrass, bentgrass, and clover would not show niche-differentiation, each of the species may be expected to be distributed equally among all management regimes, as well as equally among observation periods. This implies that in fact all observation sets of all paddocks and of all observations periods would be mere replications of each other. As the expected frequency of species combinations would then be independent of both the paddock and the time of observation, all observation sets can then be treated identically, and hence be pooled.

The calculation of these expected frequencies is here exemplified by using the pooled data of management system 3 ("lenient, non-integrated, mixed grazing"), which are listed in Table 7.1. In absence of niche-differentiation and direct competition, the fraction of quadrats in which ryegrass is expected to be ranked first and clover as second (abbreviated to **Lp Tr ***), is simply given by the product of the probability that a quadrat is dominated by ryegrass, and the probability that clover takes second rank in a quadrat. Using Table 7.1, this product equals 343 / (578-33) x 162 / 578 = 0.176, corresponding to 0.176 x 578 = 101.96 quadrats. Similarly, the expected frequency of **As Tr *** quadrats is derived by 188 / (578-33) x 162 / 578 = 0.097, corresponding to 0.097 * 578 = 55.88 quadrats. The expected frequencies of **Lp * Tr** quadrats and of **As * Tr** quadrats can be computed likewise.

Table 7.1: *Observed number of quadrats in which perennial ryegrass (Lp), creeping bentgrass (As), white clover (Tr) and other species were ranked 1st (rank 1), 2nd(rank 2), or 3rd (rank 3). Sum of all measurements of farm system 3.*

| | rank 1 | rank 2 | rank 3 | TOTAL |
|---|---|---|---|---|
| Lp | 343 | 197 | 35 | 575 |
| As | 188 | 159 | 146 | 493 |
| Tr | 33 | 162 | 162 | 357 |
| Other | 14 | 60 | 228 | 302 |
| TOTAL | 578 | 578 | 571 | |

Table 7.2: Observed quadrat frequencies (column 2), and quadrat frequencies expected under total niche-differentiation (column 3), under niche-differentiation in response to management (column 4), and in absence of any interactions (column 5). For explanation see text.

| species combination | **observed** | expected (total niche diff.) | expected (management niche diff.) | expected (in absence of interactions) |
|---|---|---|---|---|
| **Lp Tr *** | **146** | 120.9 | 117.3 | 102.0 |
| **Lp * Tr** | **97** | 100.9 | 104.7 | 102.0 |
| **Lp * *** | **100** | 121.2 | 120.9 | 139.1 |
| **As Tr *** | **14** | 37.4 | 40.2 | 55.9 |
| **As * Tr** | **62** | 56.9 | 53.1 | 55.9 |
| **As * *** | **112** | 93.7 | 94.8 | 76.2 |
| **Other** (incl. Tr * *) | **47** | 47.0 | 47.0 | 47.0 |
| **SUM** | **578** | 578 | 578 | 578.1 |

Note that the 33 clover dominated quadrats are subtracted from the total number of quadrats in which species are ranked first, as the probability of **Tr Tr *** and **Tr * Tr** quadrats is disregarded. In fact the 33 **Tr **** quadrats are allocated to the category "other" after the calculations.

Table 7.2 lists the frequencies of the species combinations as observed at management system 3 (column 2), as well as the frequencies which would have been expected in absence of niche-differentiation and direct competition (column 5).

Clearly the observed frequencies differ from the frequencies expected in absence of niche-differentiation and direct competition ($\chi^2$ - test: $p < 0.001$). In particular, the number of observed **Lp Tr *** quadrats (146) was larger than expected (102.0), whereas the number of observed **As Tr *** quadrats (14) was smaller than expected (55.9). This indicates that the species in fact did show mutual interactions, either by direct competition or by niche-differentiation.

**Expected frequencies under niche-differentiation in response to management, but in absence of direct competition.**

The niche-differentiation in response to management will be referred to as "management niche-differentiation". In case ryegrass, bentgrass, and clover are assumed to show this management niche-differentiation, yet no direct competition, the species may be expected to be distributed unequally between paddocks under a different management regime. However, an equal distribution is expected among paddocks which are managed identically, and among observation periods. For

Table 7.3: Observed number of quadrats in which perennial ryegrass (Lp), creeping bentgrass (As), white clover (Tr) and other species were ranked 1st (rank 1), 2nd (rank 2), or 3rd (rank 3). Sum of all measurements of the grazed plots of farm system 3.

| ***grazed*** | rank 1 | rank 2 | rank 3 | TOTAL |
|---|---|---|---|---|
| Lp | 101 | 115 | 20 | 236 |
| As | 129 | 65 | 33 | 227 |
| Tr | 5 | 26 | 62 | 93 |
| Other | 5 | 34 | 124 | 163 |
| TOTAL | 240 | 240 | 239 | |

Table 7.4: Observed number of quadrats in which perennial ryegrass (Lp), creeping bentgrass (As), white clover (Tr) and other species were ranked 1st (rank 1), 2nd (rank 2), or 3rd (rank 3). Sum of all measurements of the silage plots of farm system 3.

| ***silage*** | rank 1 | rank 2 | rank 3 | TOTAL |
|---|---|---|---|---|
| Lp | 242 | 82 | 14 | 338 |
| As | 59 | 94 | 114 | 267 |
| Tr | 28 | 136 | 100 | 264 |
| Other | 9 | 26 | 104 | 139 |
| TOTAL | 338 | 338 | 332 | |

management system 3, this means that all observation sets of the grazed paddocks, as well as all observation sets of the silage paddocks, are mere replications of each other. Therefore all observation sets of the grazed paddocks were pooled, as well as all observation sets of the paddocks which were cut for silage (Tables 7.3 and 7.4).

The frequency of **Lp Tr *** quadrats on the grazed paddocks which are expected under management niche-differentiation is now given by: 101 / (240-5) * 26 / 240 = 0.047, corresponding to 0.047 * 240 = 11.17 quadrats. Similarly, expected frequency on the silage paddocks equals 242 / (338-28) * 136 / 338 = 0.314, corresponding to 106.17 quadrats. Consequently, the total number of **Lp Tr *** quadrats expected on all paddocks of management system 3 equals 11.17 + 106.17 = 117.34 quadrats. The frequencies of each of the other species combinations can be computed likewise, and are given in Table 7.2 (column 4).

Table 7.2 shows that the frequencies expected under management niche-differentiation (column 4) are significantly different ($\chi^2$-test, $p < 0.05$) from the frequencies which were expected

in absence of niche-differentiation (column 5). Particularly the asymmetric distribution of bentgrass and clover among the grazed and the cut paddocks reduced the probability that these two species could be observed in quadrats simultaneously. Conversely, the fact that the presences of ryegrass and of clover were both favoured by the cutting regime (compare Tables 7.3 and 7.4), increased the likelihood that clover would be ranked second or third in quadrats dominated by ryegrass. The significant difference between the two expected frequencies indicates that ryegrass, bentgrass, and clover did show niche-differentiation in response to management.

**Expected frequencies under niche-differentiation in response to a complex of unknown factors, but in absence of direct competition.**

When it is assumed that ryegrass, bentgrass and clover do not only show management niche-differentiation, but instead niche-differentiation to a complex of unknown factors (e.g. both management and time), the species may be distributed asymmetrically among all paddocks, as well as among observation periods. This niche-differentiation in response to a complex of unknown factors will be referred to as the "total niche-differentiation". As a result, individual observation sets may no longer be treated as replications, and pooled. Therefore, the expected frequencies under total niche-differentiation were first calculated for each individual observation set of management system 3. The sum of these expected frequencies is listed in Table 7.2 (column 3).

Table 7.2 shows that the differences between the quadrat frequencies which were expected under management niche-differentiation (column 4) and the frequencies expected under total niche-differentiation (column 3) are small, and not significant ($\chi^2$-test, $p > 0.05$). This indicates that the ryegrass, bentgrass, and clover showed niche-differentiation only in response to the management regime, and not additionally in response to any other factors, such as time.

**Segregation of direct competition and niche differentiation**

Summarising, four quadrat frequency distributions have been computed:

1) The observed quadrat frequencies give the incidences of specific combinations of dominant, second and third species. These frequencies are subject to both direct interactions between species and to niche differentiation. Therefore species may be distributed asymmetrically both within and between paddocks.

2) The expected quadrat frequencies under total niche-differentiation, assuming that plant species do not show direct interactions within paddocks, but may be distributed asymmetrically between individual paddocks and observation periods. The difference between these expected frequencies and the observed frequencies consequently defines the direct interactions between plants within paddocks.

3) The expected quadrat frequencies, assuming that plant species do not show direct interactions within paddocks, but are distributed asymmetrically between paddocks under identical management regimes.

4) The expected quadrat frequencies, assuming a fully equal distribution of plants species between and within paddocks and observation periods. The difference between these last two expected frequencies therefore defines the specific niche differentiation in response to management between plant species.

The observed quadrat frequencies and the various expected quadrat frequencies of Table 7.2 are illustrated in Figure 7.2. This figure presents the number of observed and expected ryegrass and bentgrass dominated quadrats, marked "Lp" and "As", respectively, in which clover was ranked second (black bars), third (grey bars), or absent (white bars). The observed number of ryegrass dominated quadrats in which clover was present, is clearly larger than the number expected in absence of niche-differentiation and direct competition. The opposite is found for quadrats dominated by bentgrass.

Figure 7.2 also shows that these differences can partly be explained by the management niche-differentiation, as the differences between the quadrat frequencies expected in absence of interactions ("exp none") and the frequencies expected under management niche-differentiation ("exp man") were significant (dashed bars in Figure 7.2). This means that bentgrass and clover were asymmetrically distributed among the grazed and the silage paddocks. This reduced the probability of their simultaneous presence in the quadrats, regardless of direct competition.

Hardly any differences occurred between the quadrat frequencies expected under management niche-differentiation ("exp man") and under total niche differentiation ("exp niche"). This implies that the species were only differentiated in response to the management, and not to any other factor, such as time.

However, there was a significant difference ($\chi^2$-test, $p < 0.025$) between the observed quadrat frequencies and the frequencies expected under total niche-differentiation. Calculating these expected frequencies, it was taken into account that bentgrass was mainly present on the grazed paddocks, whereas ryegrass and clover mainly occurred on the silage paddocks, and that the species may be present during different observation periods. Nevertheless, an even smaller number of **As Tr *** quadrats was observed than expected under total niche-differentiation. This means that bentgrass and clover did not only prefer different management regimes, but additionally "avoided" each other by direct competition (crossed bars in Figure 7.2).

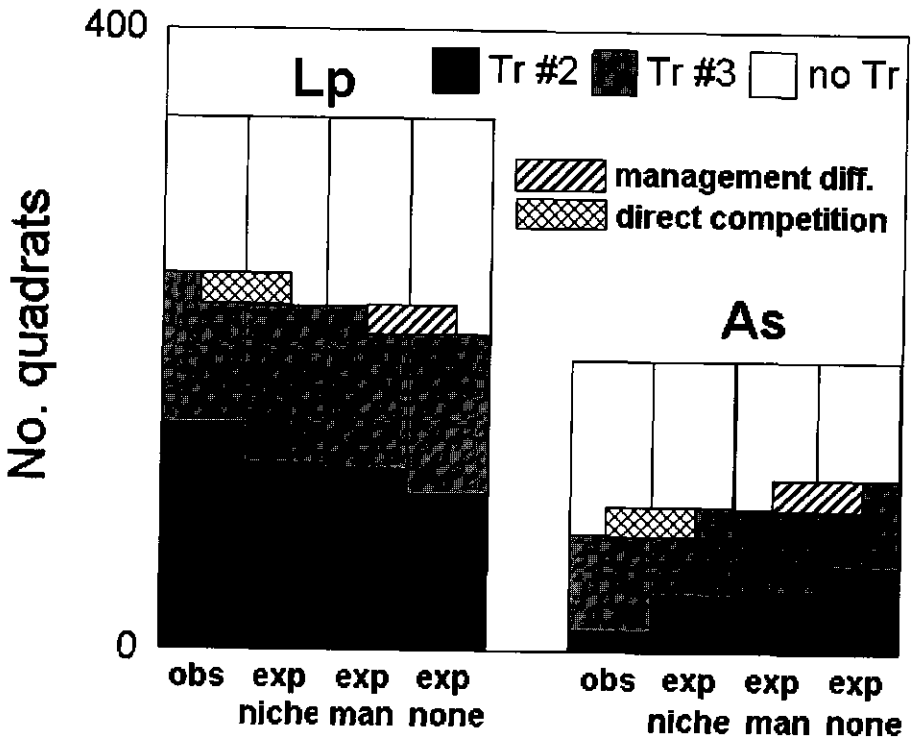


Figure 7.2: Quadrat frequencies which were observed (obs), and which would be expected under total niche-differentiation (exp niche), under management niche- differentiation only (exp man) and in absence of interactions between species (exp none). For explanation see text.

## 7.3 Results and discussion

Under management system 3, white clover appeared less frequently, both in relative and absolute terms, in patches which were dominated by creeping bentgrass, than it did in ryegrass dominated patches. This was simultaneously the result of the niche differentiation in management, and the direct competition between these two species. In other words: the cutting regime favoured clover growth, whereas lenient grazing stimulated bentgrass, but wherever bentgrass dominated, it tended to exclude the clover by direct competition. In bentgrass dominated quadrats in which clover appeared, it was usually ranked third, and only rarely as second. Instead perennial ryegrass and clover showed converse interactions: these two species actively preferred the same management niche, i.e. a cutting regime, and also showed a positive direct interaction. In fact clover was present in more than two thirds of the patches dominated by ryegrass.

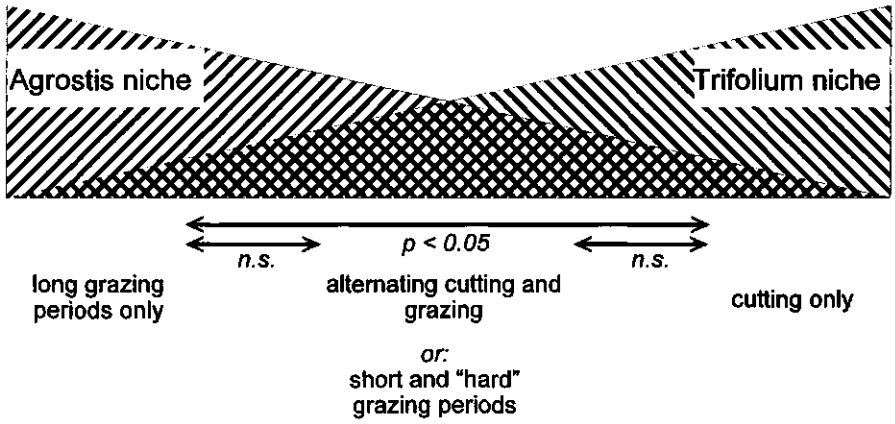


Figure 7.3: Simplified visualisation of the niches of white clover and creeping bentgrass, along a one-dimensional management axis.

*7.3. 1 Niche-differentiation*

In fact the grassland management system which has been dealt with so far, i.e. the lenient, non-integrated cutting and mixed grazing (management system 3), was the only system in which perennial ryegrass, creeping bentgrass and white clover showed differentiation in response to management, or showed any niche-differentiation in general. No niche-differentiation was observed between any of the other grassland management systems, which means that the frequencies of ryegrass, bentgrass, and clover were *indifferent* to the following contrasting management aspects:

1) cutting only vs. alternating cutting and grazing
2) grazing only vs. alternating cutting and grazing
3) mixed grazing vs. sheep grazing
4) mixed grazing vs. cattle grazing
5) sheep grazing vs. cattle grazing
6) "hard grazing" (short grazing periods of 1 to 3.75 weeks) vs. "lenient grazing" (long grazing periods of 7.5 weeks)
7) cutting only vs. hard grazing only.

Notably, there was no niche-differentiation to the last management aspect, i.e. cutting only vs. hard grazing only. This contrasts with the significant niche-differentiation between the cutting only regime and the lenient grazing only regime. Arguably, the effects of hard grazing on the botanical composition of the paddocks were more similar to the effects of a cutting event (Chapter

6; see also Evans *et al.*, 1992). Apparently, the cutting only regime and the lenient grazing only regime mark the management niche boundaries of creeping bentgrass and white clover, respectively, with all other grassland management regimes located between these extremities, which is visualised in Figure 7.3.

The increased performance of white clover under a cutting regime or under a regime of infrequent and hard grazing, as opposed to a regime of frequent tissue removal, has been well documented (e.g. Hay *et al.*, 1989; Evans *et al.*, 1992; Laws & Newton, 1992; Fothergill *et al.*, 2000; De Wolf & Schulte, *in prep.*).

The preference of creeping bentgrass to grow under frequent, lenient grazing instead, is less well understood. Sheldrick *et al.* (1990) compared swards dominated by ryegrass and bentgrass, respectively, for a range of fertiliser treatments under a cutting regime. They found a higher persistency of bentgrass than of ryegrass, especially under low nitrogen inputs (0 and 200 kg $ha^{-1}$ ), in spite of its consistently lower production. This could, however, be related to the poor drainage of the soils on which their experimental sites were located, as creeping bentgrass prefers a relatively humid environment (Kik *et al.*, 1990), which is in fact another aspect of its niche, that has not been dealt with here. Alternatively, it could be a result of the high, i.e. monthly, cutting frequency, which in fact approaches the cutting frequencies used for simulated grazing. Using the same cutting frequency, however, Frame (1990) instead found a decreasing production of a bentgrass dominated sward over a three year period.

In the current experiment, the increase of bentgrass on the paddocks which were exclusively grazed for long periods could possibly be related to its continuous elongation of vegetative stems, decreasing its digestibility (see also Sheldrick *et al.*, 1990). Lodging of these stems was visually observed during the grazing periods, which arguably reduced its palatability and accessibility, and hence the intake by the grazing animals. Parsons *et al.* (1994) showed that, especially under lenient and long grazing periods, animals may exploit their preference for the most palatable plant species, as they are able to select continuously for its regrowing tissue. This eventually results in a competitive advantage of the less palatable species. Further experimental research is required to elucidate the morphological and physiological responses of creeping bentgrass to a range of grazing regimes.

*7.3.2 Direct competition*

Also for all *individual* observation sets of *all* management systems, the quadrat frequencies expected under total niche-differentiation were calculated as above, and summed. This expected frequency distribution showed highly significant differences with the observed quadrat frequencies ($p < 0.001$). Indeed white clover was less frequently observed in bentgrass dominated quadrats than would be expected, had these species been distributed equally *within* each paddock (Figure 7.4).

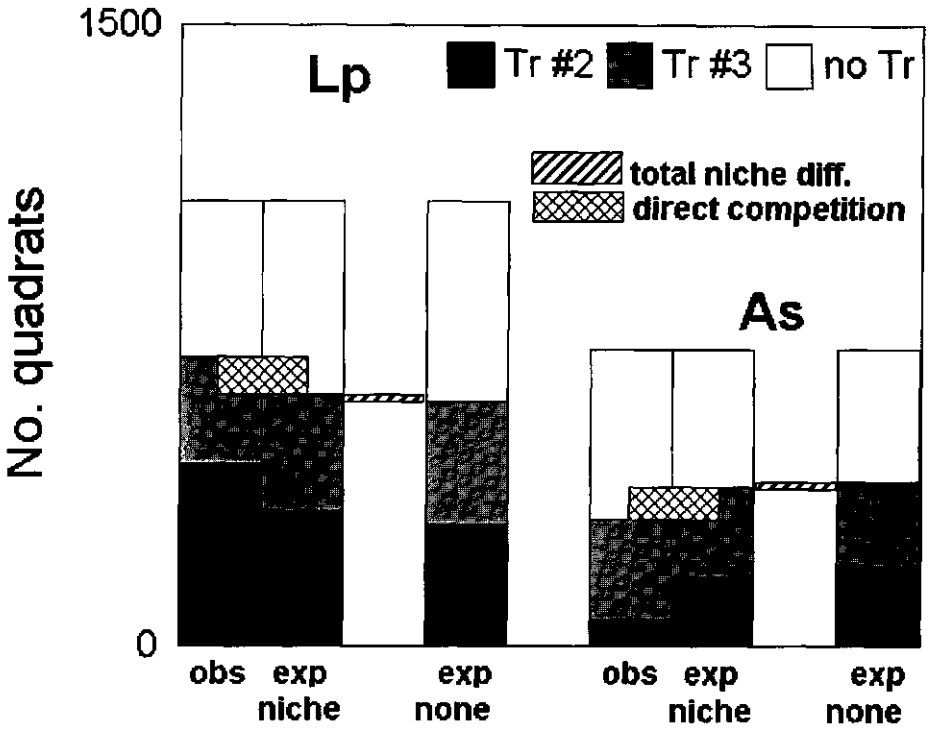


Figure 7.4: Quadrat frequencies of all observation sets of all plots, which were observed (obs), which would be expected in presence of total niche differentiation (exp niche), and in absence of niche-differentiation and direct competition of plant species (exp none). For explanation see text.

Especially the number of bentgrass dominated quadrats in which clover was marked second, was well below the expected number (66 observed quadrats vs. 169 expected), which suggests that clover performance was indeed reduced by direct competition with bentgrass. It could be argued that the low incidence of **As Tr** * quadrats resulted instead from small-scale niche-differentiation *within* the paddocks, with respect to the heterogeneity of the soil nitrogen status, caused by the deposition of faeces and urine. However, the same extent of direct clover exclusion was observed on the silage paddocks, on which this heterogeneity may be assumed absent.

The mechanisms through which bentgrass excludes clover are largely unknown, but could be related to the dense growth habit of the former species. Gilliland (1996) studied the compatibility of perennial ryegrass cultivars with white clover cultivars, relating differences between clover survival rates to ryegrass cultivar characteristics. He identified sward density as the overriding factor determining clover vigour, with the highest clover survival rates in open ryegrass swards. These findings agree with Frame (1990), who compared the compatibility of white clover with a range of grass species under simulated grazing. He reported exceptionally low yields and clover contents in

mixtures with creeping bentgrass, and related these to the dense tillering of the latter. Indeed Sheldrick *et al.* (1990) also observed a lower percentage of bare ground in the bentgrass dominated swards, especially under low nitrogen inputs (0 and 200 kg $ha^{-1}$).

*7.3.3 Implications for grassland management*

Summarising, in the current experiment the niches of perennial ryegrass, creeping bentgrass and white clover with respect to management and seasonality were largely found to overlap. Only between the two management extremities, i.e. semi-continuous defoliation vs. infrequent cutting, did the niches significantly differ. At the same time, clover was directly excluded on bentgrass dominated patches, under all management regimes. This has serious implications for the grassland management, as apparently bentgrass is not merely an indicator species of sub-optimal management. Only on the silage paddocks, bentgrass performance was compromised by management, in favour of white clover. The results of this experiment therefore suggest that a sequence of silage cuts may be the only tool to reduce the bentgrass content in extensively managed grassland, and that bentgrass infested fields should not be grazed leniently for prolonged periods.

Care should be taken with the alternative approach of reseeding infested pastures, as Sheldrick *et al.* (1990) noted that bentgrass benefits from disturbed soil conditions. Their bentgrass dominated swards had established spontaneously on a field which had frequently been tilled in previous years. The field used in the current experiment had a similar life history, as it had been used for the production of cereals and arable silage for a number of years before reseeding.

*7.3.4 Methodology*

The new methodology presented in this chapter was used successfully to discriminate between direct and indirect interactions between plant species, based on existing DWR observations. In fact it uses the information, concealed within the specific combinations in which plant species occur in quadrats, to its full extent. However, the limitations of the methodology should be kept in mind.

Most importantly, it should be noted that the quantification of the niche-differentiation and competition is relative to the mixture of species observed, in this case perennial ryegrass, creeping bentgrass and white clover, and to the environment. In other mixtures different or even converse interactions may be observed. In the current experiment, for instance, clover was observed in only 6 of the 31 quadrats which were dominated by Yorkshire fog (*Holcus lanatus*). It is conceivable that in a mixture of Yorkshire fog, creeping bentgrass and clover, the latter would actually be observed *more* frequently than expected in bentgrass dominated patches, as the clover exclusion by the first species would be even stronger. Comparing the clover-compatibility of companion grasses, Frame (1990) also reported lower clover contents in swards dominated by Yorkshire Fog than in those

dominated by creeping bentgrass. Therefore it can only be concluded from the current experiment that the exclusion of clover by bentgrass is stronger than its exclusion by ryegrass.

Additionally, the local environment may also define the mutual interactions between the plant species. The concept of niches is multi-dimensional, and interactions between various aspects of niche-differentiation may not be assumed negligible. In other words: the observed niche-differentiation towards grassland management may be altered in a different environment, e.g. on wetter soils, as the conflict between the results of the current experiment and those of Sheldrick *et al.* (1990) suggests.

Secondly, in the current format in which the various expected frequencies were calculated, frequencies were also attributed to hypothetical quadrats in which one species occupies more than one rank, e.g. both first and second rank. Although the "cumulative ranking method" (Jones & Hargreaves, 1979) allows for these quadrats also to be observed in the field, it is felt that these expected hypothetical quadrats are in fact artefacts of the methodology. However, as this format reduced the expected number of bentgrass dominated quadrats in which clover was ranked second or third, it only made the methodology more conservative, which means that the null-hypothesis that niche-differentiation and competition are *not* present, was less easily rejected. An alternative format was also applied to compute expected frequencies, which did not attribute probabilities to quadrats in which a species occupied more than one place. However, using this format, more quadrats with clover present were expected than were actually observed, which was considered to be more inconsistent.

Finally, in the current format clover dominated quadrats were pooled in the category "other". As in the current experiment these quadrats were low in number, this did not significantly affect the results. Nevertheless, in grasslands in which clover is dominant more frequently, this could lead to a loss of information on the interaction between grasses and clover in clover dominated patches. Therefore the current methodology should only be used in pastures in which clover competes with two or more dominant species. In other cases, preference should be given to the observation and calculation of the number of quadrats in which combinations of plant species are simply present, regardless of their ranking order. In that case point quadrats may also be used to establish the frequencies of these combinations.

The DWR and point quadrats have already been used in a large number of experiments in order to establish botanical compositions (e.g. 't Mannetje & Haydock, 1963; Jones & Hargreaves, 1979). The methodology presented in this chapter can be applied to these existing databases. Subsequently, the niche-differentiation between perennial ryegrass, white clover, and creeping

bentgrass in response to other aspects of grassland management, as well as direct competition between these species, can be analysed for a wide range of environments. These analyses could rapidly provide more insight into the mechanisms the mutual interactions between these plant species, and therefore prove a valuable tool in the management of mixed pastures.

# Chapter 8: General discussion

## 8.1 The philosophy of grassland stability

*8.1.1 The complexity of ecosystem stability*

Originally, the current study set out to understand the factors which underlie the production stability of mixed grasslands. It was aimed to comprehend stability by a minimum number of key-factors which regulate the delicate balance and interactions between grassland species. Consequently, it was envisaged to develop a universal set of grassland management tools, with which the production stability of mixtures of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) would be safeguarded (Chapter 1). After all, this reductionistic approach had indeed been employed successfully to identify single ecosystem properties as well as management tools which define and encourage the productivity of clover-driven grasslands on the short term. Many examples of these properties and management tools, reported in the literature, have been discussed in detail in this thesis.

However, the present study has demonstrated that the production stability of grassland ecosystems, as opposed to their production levels, cannot be fully understood by the analysis of processes in isolation only. Instead, grassland stability encompasses the balance between species, which results from the sum and the mutual interactions between individual ecosystem properties, management aspects, and the environment. Some examples have been given to illustrate these mutual interactions. In Chapter 2, it was shown how both the clover content and the stability of grazed swards depended on interactions between preferential grazing, the stocking density and plant escape mechanisms (Figure 2.11 in Chapter 2). In Chapter 3, it was demonstrated how the intrinsic ecosystem properties showed interactions with structured and stochastic fluctuations of environmental variables, as the impact of these fluctuations on intrinsically stable systems differed from their impact on intrinsically unstable systems. Structured and stochastic environmental fluctuations additionally showed mutual interactions (Figure 3.3 in Chapter 3). In Chapter 6, the spatial heterogeneity of mixed swards was defined by interactions between urine depositions, niche-differentiation, synchronisation of defoliation, plant escape mechanisms, selective grazing, and the instantaneous grazing pressure. Moreover, these interactions had opposite effects on the spatial heterogeneity of the total herbage mass on the one hand, and of the clover herbage mass on the other.

Matters are further complicated, as all ecosystem processes and properties are subject to change over time, thereby changing their interactions. The dynamic behaviour of ecosystem

variables does not necessarily result exclusively from their responses to environmental fluctuations. Additionally, variables may continue to change in response to each other. The simple simulation model in Chapter 2, as well as the models by Schwinning & Parsons (1996a) and Thornley *et al.* (1995), showed that the delayed response of only one variable (the mineral nitrogen pool) may cause perpetual changes of all other variables of the ecosystem.

Additionally, the ecosystem processes and properties, as well as their responses to each other and to the fluctuating environment may not only change over time, but additionally may differ spatially between neighbouring patches. This spatial heterogeneity may give rise to further interactions between processes, taking place in different patches. These spatial interactions may arise from the movement of clover stolons (Schwinning & Parsons, 1996b), but may additionally be mediated by the grazing animal. In Chapter 6, for instance, it was argued that the defoliation frequency of a patch depends on e.g. the botanical composition of other patches. As suggested in Chapter 2, and as shown in Chapters 4 and 6, these spatial interactions may lead to a stable herbage production at field scale, in spite of the unstable production of individual patches. Therefore, grassland ecosystems at field scale may exhibit what some authors (e.g. Silvertown, 1980) refer to as *emergent properties* over grassland ecosystems at patch scale.

Finally, grassland ecosystems, as well as their stability, may change entirely when the invasions by "third species" into mixtures of perennial ryegrass and white clover are taken into account. Chapter 7 demonstrated how the performance of white clover was severely compromised by an invasion of creeping bentgrass (*Agrostis stolonifera*). This reduction in clover growth will almost certainly have had consequences for the nitrogen dynamics of the grassland ecosystem, and therefore may have changed the behaviour of the entire ecosystem itself.

Consequently, the stability of grassland yields between years depends on every process on every patch under every weather condition at every moment of production. Evidently, stability can then only be understood by appreciating the complexity of processes within grassland ecosystems, and their interactions with the environment, with spatial dimensions, and with time.

### *8.1.2 The dynamics of ecosystem stability*

In light of the above, grassland ecosystems are arguably more likely to manifest dynamic rather than static behaviour, which had already been suggested by the latest grassland simulation models (Thornley *et al.*, 1995; Schwinning & Parsons, 1996a,b; Thornley 1998). In the present study, this dynamic behaviour was also identified in "real" ecosystems. In Chapter 6, grassland plants showed rapid and complex responses to a change of management, and even to a management factor as simple as the topping of the sward. Also the extrinsic instability of all experimental plots under a cutting regime in the Park Grass Experiment (PGE) and in the Ossekampen experiment suggests that the behaviour of these experimental ecosystems was far from

static. In fact, Silvertown (1980), Dodd *et al.* (1994) and Silvertown & Dodd (1995) all detected and reported on dynamic changes of the botanical composition of the ecosystems at the PGE in more detail.

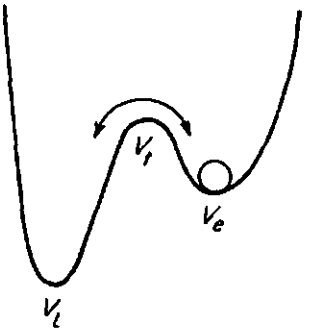


Figure 8.1: A metaphor of grassland stability, presented by Noy-Meir (1975; his Figure 6). For explanation see text.

Interestingly, the experimental ecosystems were stabilised to some extent either by the regular applications of lime, or by grazing (Chapter 4). It was argued that lime applications would increase the nitrogen mineralisation rates by stimulating soil life, whereas grazing would lead to spatial heterogeneity and an accelerated recycling of nutrients. It is interesting to note that both lime applications and grazing hence led to stability by *increasing* the dynamic behaviour of the grassland ecosystems. As a result, stable ecosystems may be far from synonymous, if not antonymous, with static ecosystems. In Chapter 2, it was already tentatively noted that Oldeman (1990) came to similar conclusions for forest ecosystems. His term ecuilibrium (from eco-equilibrium) was used to describe ecosystems which are stabilised by their dynamic behaviour at lower hierarchical or spatial levels, which resembles the term "dynamic equilibrium", used by Silvertown (1980).

*8.1.3 The concept of grassland stability*

The picture painted above contrasts sharply with the notion that stable ecosystems would be characterised by one or more "steady-states", in which all ecosystem variables remain constant, or follow identical seasonal patterns between years (e.g. Noy-Meir, 1975, Grenfell, 1988; Thornley, 1998, but see also Schwinning & Parsons, 1996a). This notion obviously originates from studies in which ecosystem stability is analysed by means of simulation models. Simulated ecosystems are usually placed in either a constant or a sinusoidally fluctuating environment, and all simulated grassland ecosystems observed in the literature were subjected to a constant management regime only. Moreover, no simulation model was found in which the biotic environment, i.e. invasions by other plant species, was taken into account. In these static abiotic, biotic, and managerial environments, "attractive" equilibria may indeed arise, in which processes are in perpetual balance, and to which the ecosystem returns after an individual disturbance.

This conceptualisation of ecosystem stability was illustrated graphically by Noy-Meir (1975), who used the well-known ball in a hill landscape as a metaphor for the stability of continuously grazed monocultures of grass (Figure 8.1, which is his Figure 6). His ecosystem showed two equilibria, one at a low and one at a high herbage mass, in which the animal intake rate continuously equalled the herbage production rate. These two equilibria correspond with the two

valleys in Figure 8.1, in either of which the ecosystem (the ball) is located. The ball may be "pushed" out of the valley temporarily by a once-off environmental disturbance, but will roll back to its equilibrium after this event. Hence this equilibrium is classified as "locally attractive". In the event of a large environmental disturbance, the ecosystem may be "pushed over the hill", and consequently roll into a new equilibrium. The shape of the landscape is here defined by the constant environment and the constant management regime.

A different concept of grassland stability arises from the current study. It was shown that fluctuating yields may either result from internal ecosystem oscillations, or from system responses to environmental fluctuations. A distinction was made between extrinsically stable systems and extrinsically unstable systems. The latter are characterised by yield oscillations in an environment which shows seasonal, but no stochastic fluctuations. These internal oscillations are caused by the capacity of the ecosystem to change its own soil environment, most prominently illustrated by the impact of the nitrogen fixation by white clover on the soil nitrogen levels. However, these internal oscillations were also observed, be it to a lesser extent, on experimental plots receiving NPK fertiliser, which suggests the existence of additional self-changing processes. In any case, these extrinsically unstable ecosystems were rarely further destabilised by stochastic environmental fluctuations. In fact, these stochastic fluctuations instead stabilised the yield patterns on average. These findings led to the conclusion that extrinsically unstable systems exhibit a negative sensitivity to the variability of the environment (Figures 4.1 and 4.6).

Instead, extrinsically stable ecosystems are characterised by their constant production in an environment showing structured fluctuations. This stability is either the result of accelerated nutrient flows, enabling a balance of counteracting processes such as the competition for light and niche-differentiation, or the result of compensatory herbage production between patches. However, it was demonstrated in Chapters 2, 3 and 4 that these extrinsically stable ecosystems show a positive sensitivity to stochastic environmental fluctuations.

In conclusion, the extrinsic stability level of ecosystems is inversely related to its sensitivity to environmental variability. It was hypothesised in Chapter 3, and demonstrated in Chapter 4, that this paradox reduces the differences between the actual stability levels of extrinsically stable and unstable systems. In fact, it was predicted (Figure 3.3 in Chapter 3) that in highly variable environments, extrinsically unstable systems may show a more constant herbage production between years than extrinsically stable systems.

From a practical point of view, the constancy and hence reliability of grassland production can consequently not be achieved merely by an increase of the extrinsic stability. Instead, both the extrinsic stability and the sensitivity of grassland ecosystems need to be addressed simultaneously

to this purpose. The management required to enhance the extrinsic stability of grasslands arguably differs from the management aimed at the reduction of their sensitivity. Therefore it is tentatively proposed to discriminate two complementing management strategies, referred to as "structural" and "dynamic" management strategies, respectively, to ensure high actual stability levels of mixed grasslands. These will be discussed below.

## 8.2 Management strategies for mixed grasslands

### *8.2.1 Structural management strategies*

Increasing the extrinsic grassland stability by management requires an understanding of the ecological processes involved. Due to the interactions between processes, exemplified above, managerial attempts to control one process, may lead to unforseen responses from other. For example, using large-leaved clover varieties in an attempt to improve its competitiveness in the competition for light with grasses, may jeopardise its escape mechanisms, exposing it to selective grazing, and hence compromise its performance (Figure 2.11 in Chapter 2). Therefore the role of short-term experiments in prototyping grassland management systems is questionable, in case the *effect of one management tool on one ecosystem process is studied in isolation*. This was exemplified by the diverging results of two studies which both studied the impact of the stocking rate on clover performance (Chapter 2). It was argued that this divergence was possibly the result of the two different clover varieties used in these two experiments. Moreover, it was shown that the actual stability levels of ecosystems, measured in these short-term experiments, is strongly dependent on the coincidental environmental fluctuations during the observation period. Largely different levels of actual stability may be monitored during other years (Chapter 3).

More conclusive evidence was instead given by the two long-term experiments dealt with in this thesis, i.e. the Park Grass Experiment (PGE) and the Ossekampen. The long time-span over which the ecosystems in these experiments have been managed and monitored, allowed for the segregation of the extrinsic stability level and the sensitivity of each individual ecosystem. The extrinsic stability level encompasses the effects of individual management tools on *all* ecosystem processes (Chapters 3 and 4). From these two experiments, grazing, lime applications, and to a much lesser extent fertiliser applications were identified as structural management tools which increase this extrinsic stability level.

#### Grazing

The ecosystems which arose under a grazing management in the Ossekampen experiment

were the only ecosystems observed, which were entirely or at least nearly extrinsically stable. It was explained how the stabilising effects of grazing may result from the accelerated recycling of nutrients, the lower herbage masses, and the spatial heterogeneity (Chapter 4). The relative importance of each of these associated effects in stabilising the ecosystem is difficult to establish. Some indirect suggestions were derived from the lower stability of the ecosystem in the PGE which received farmyard manure (FYM) compared to the ecosystem which received equal rates of mineral nitrogen (Chapter 4). Whereas the FYM plot was assumed to display a higher degree of spatial heterogeneity, the overall availability of nutrients was deduced to be higher on the fertilised plot. The higher extrinsic stability level of the fertilised plot then tentatively implies that this nutrient availability has a stronger impact on the extrinsic stability level than the spatial heterogeneity.

The spatial heterogeneity is possibly the cause of the low sensitivities of the grazed ecosystems instead. Sivertown & Dodd (1994) showed that the PGE plots which did not receive nitrogen fertiliser showed a stronger response to spring rainfall, which they explained by the dependence of these ecosystems on the nitrogen mineralisation rate. In Chapter 6 it was shown that grazing, and in particular strip-grazing, led to an increased heterogeneity of the clover herbage mass, which was explained by the heterogeneity of the soil nutrient status arising from the "concentration" of nitrogen in urine and manure patches. Combining these two findings it is conceivable, though speculative, that the herbage production on urine patches and the herbage production on nitrogen depleted patches showed diverging responses to stochastic environmental fluctuations. This "spatial compensation" may be the cause of the low sensitivity at field scale of the grazed plots at the Ossekampen to the environmental variability .

**Lime applications**

The importance of nutrient availability was underlined by the higher extrinsic stability of the limed plots of the PGE, as compared to their unlimed counterparts (Chapter 4). It was argued that this higher stability resulted from the accelerated nitrogen mineralisation rates, shortening the delay between nitrogen fixation and availability. However, lime applications also improved the stability of plots receiving mineral nitrogen, in which the dependence of plant growth on the nitrogen mineralisation rate may be assumed to be small (Silvertown, 1980). This suggests that lime applications may additionally improve ecosystem stability through other pathways, such as an increase in the availability of other nutrients.

**NPK fertiliser applications**

Nitrogen dynamics have received much attention as a potential cause of extrinsic instability of mixed grasslands (Thornley *et al.*, 1995; Schwinning & Parsons, 1996a,b). The simple simulation model in Chapter 2, as well as the more sophisticated models by Thornley *et al.* (1995) and by

Schwinning & Parsons (1996a), related instability to the delayed dependence of grass on white clover for its nitrogen supply. They predicted that nitrogen fertiliser applications would conversely transform mixed grasslands into extrinsically stable grass monocultures.

The data from the PGE and the Ossekampen confirm that nitrogen applications indeed result in grass monocultures. In the Ossekampen, currently the legume presence frequency does not exceed 1% on plots receiving nitrogen fertiliser. However, in both experiments, these fertilised monocultures were neither extrinsically stable. In the Ossekampen, no relation was observed between the fertiliser regime and the extrinsic stability of the ecosystems, while this relation was weak and inconsistent in the PGE, despite the large impact of fertiliser on the botanical composition. Although the extrinsically stability was somewhat higher on the plots receiving all major nutrients (NPK), it was lowest on the plots receiving nitrogen only. Interestingly, the plot receiving all major nutrients at *low* rates (48 kg of nitrogen $ha^{-1}$ $yr^{-1}$) was almost extrinsically stable. Bearing in mind the inconsistency of these responses to nitrogen fertiliser, it is conceivable that these low external nitrogen inputs could "break" the botanical cycle arising from the nitrogen dependence of grasses on clover, without raising the soil mineral nitrogen to levels unsustainable for legumes.

Similar inconsistencies were observed in the response of ecosystems to phosphorus (P) and potassium (K). In the cutting experiment at the Ossekampen, P and K applications drastically improved clover performance, as they led to a doubling of the clover presence frequencies from 38% in 1958 to 76% to date. On the unfertilised control plots, these frequencies dropped to under 5% instead. In spite of this large difference in botanical composition, the extrinsic stability levels of the PK plot and the control plot, as well as their sensitivity, were almost identical.

Clearly, the triangular relations between the fertiliser regime, the botanical composition and the extrinsic stability of ecosystems are in need of further clarification.

**Mixed vegetations**

Although the applicability of the results of short-term experiments to prototype management tools is questionable (see above), they can be useful when put in the context of an ecosystem by using simulation models. The model presented in Chapter 2 unequivocally confirmed the stabilising effects of niche-differentiation, as reported in the literature, on entire ecosystems.

It was explained that niche-differentiation comprises the partially separate usages of resources by species. Apart from the separate nitrogen sources of white clover and grasses, which has been dealt with extensively, resources may be separated either in time or in space. Culleton *et al.* (1986) compared mixtures of early, medium-late and late perennial ryegrass varieties Ruanui, Talbot and Vigor with monocultures of each of these varieties, over three successive years. The mixtures showed a stable yield between these years, whereas each year a different monoculture showed the highest yield. The authors related this stable productivity of mixtures to the

differentiation in tolerance to temporary environmental stress-factors, as a result of which each variety compensated for the lack of growth of its companion species under various environmental conditions. Therefore the sensitivity to stochastic environmental variability was arguably reduced by this niche-differentiation in time.

Alternatively, spatial niche-differentiation was studied by R.P. Collins (*pers. comm.*), who found a higher compatibility of perennial ryegrass and white clover varieties which exhibited different rooting patterns.

Additionally, it was explained in Chapter 2 (Figure 2.11) that the stability of grazed mixtures depends to a large extent on the escape mechanisms of plants. It was argued that small-leaved clover varieties gave rise to extrinsically stable systems, whereas the use of large-leaved varieties resulted in oscillating clover performances. This was confirmed by data by Evans *et al.* (1992), who found a higher persistency of small-leaved clover varieties under grazing. Conversely, a higher persistency of large-leaved varieties was observed under a cutting regime by both Evans *et al.* (1992) and Nassiri (1998). In fact these diverging responses indicate that small-leaved and large-leaved clover varieties show a mutual niche-differentiation in response to management.

Consequently, it is conceivable, though at this stage still speculative, that an increased extrinsic stability and a lower sensitivity can be obtained by sowing mixtures of early and late varieties of perennial ryegrass, and small-leaved and large-leaved varieties of white clover, while maximising the diversity of rooting patterns.

*8.2.2 Dynamic management strategies*

Due to the positive sensitivity of extrinsically stable ecosystems to the stochastic environmental variability, in fact *all* grassland ecosystems analysed in this study showed fluctuating yield patterns. Therefore, it is tentatively proposed here that the counteraction of these yield fluctuations requires a dynamic management strategy, when the actual yield variability is not the result of a high extrinsic yield variability. In other words, fluctuations of e.g. the botanical composition which are caused by environmental conditions may be counteracted by short-term managerial measures. Numerous studies were found in the literature which reported on short-term responses of white clover and perennial ryegrass to single management factors. In Chapter 2 it was summarised that the clover performance can be rapidly enhanced by the cutting of the sward (Evans *et al.*, 1992; Fothergill *et al.*, 2000), and by omission of nitrogen fertiliser (Curll *et al.*, 1985; Barthram *et al.*, 1992; Nassiri, 1998). Additionally, higher clover contents resulted from rotational over continuous grazing by sheep, while clover grazed by cattle outperformed clover grazed by sheep (Evans *et al.*, 1992). Under sheep grazing, clover production may be sustained under a

management of strip-grazing (Chapter 6; Laws & Newton, 1992; De Wolf & Schulte, *in prep.*). Infestations of creeping bentgrass may be nullified by a sequence of silage cuts (Chapter 7).

Due to the stochastic nature of the environment, and due to the fact that each individual grassland ecosystem is unique with respect to e.g. its species, varieties, soil types, mineralisation rates, stocking rates, weed invasions, *etcetera*, the dynamic management required to counteract short-term fluctuations cannot be generalised in advance by prototypical management systems. Instead, this dynamic management entails a continuous and active intervention to "adjust" the ecosystem, in order to maintain the desired balance between species, and hence the desired production level. Obviously, this dynamic management does not only compel an understanding by each individual farmer of the dynamic management tools listed above, but additionally a familiarity with his ecosystem and its history.

*8.2.3 Management systems at farm level*

Ultimately, an integration of structural and dynamic management strategies is required for the implementation of grassland management systems at farm level. It is at this level that farmers operate, and at which stability of production is eventually required. It cannot be overstressed that the requirements for achieving stability at farm level may differ from those for achieving stability at field level. Stability at field level, for instance, was maximised under a grazing regime, and low under a cutting regime. However, grazing animals are commonly housed during winter in North-West Europe, which commands the cutting of swards for winter feeding. Consequently, an attempt to increase the stability of herbage production between years by maximising the grazed area, may jeopardise the constancy of the feed supply within years. Conversely, conserving larger quantities of grass, to be utilised during periods of adverse growth conditions, may increase the flexibility and hence the reliability of the feed supply within years. Similarly, it was suggested that even when pastures manifest intrinsic yield oscillations, stability at farm level may still be achieved by setting entire fields "out of phase" with each other (Chapter 2).

Additionally, the desirability of a stable herbage production may be in conflict with the economic imperative to maximise the level of herbage production. For instance, the use of small-leaved clover varieties, and the minimisation of nitrogen fertiliser applications may compromise the total productivity of swards. Likewise, the implementation of strip-grazing in order to maintain stability under sheep grazing may challenge the economic productivity at farm level, due to the high fencing costs involved.

However, productivity and production stability need not necessarily be mutually exclusive, as both may be enhanced simultaneously by e.g. applications of lime. The development of

additional management strategies which simultaneously address the stability and productivity of mixed grasslands is indeed an interesting challenge.

## 8.3 Recommendations for further research

*8.3.1 Development of simulation models*

It has been exemplified that ecosystems may show complex responses to single management factors, resulting from mutual interactions between internal processes. Additionally, it has been argued that these responses may consequently be unique and confined to a particular ecosystem at a particular location. Therefore, the stability of ecosystems can hardly be understood from short-term experiments, in which the effect of only one process or management tool is studied. Instead, simulation models provide a tool to comprehend and analyse these complex interactions, as demonstrated in Chapter 2. Moreover, simulated ecosystems can be subjected to a wide range of structured and stochastic environmental regimes, which enables the prototyping of individual management systems for grasslands on e.g. different soil types and under a range of meteorological conditions.

In Chapter 2 it was suggested that simulation models may only satisfactorily reflect ecosystems when the spatial heterogeneity of grasslands is taken into account. The interactions between plant species, as well as the interactions between plants and the grazing animals depend on both the vertical (Chapter 5) and the lateral (Chapters 2, 6, 7) distribution of herbage. Consequently, the accuracy of simulations in which the herbage mass of each species is assumed to be uniformly distributed across the entire field, is highly questionable. Therefore the development of spatially explicit simulation models may be mandatory to achieve accurate representations of mixed grasslands. The simulation of the horizontal sward structure has already been realised by to use of a cellular automaton (Schwinning & Parsons, 1996b), which entails the subdivision of pastures into numerous discrete patches of identical sizes. Additionally, a complementary mechanistic model was presented in Chapter 5, which enabled the prediction of the vertical sward structure from the morphologies of perennial ryegrass and white clover.

Furthermore, it has been demonstrated that the output of simulation models is at least partly predefined by their structure (Chapter 2). For instance, the stability level of ecosystems was associated with the nitrogen dynamics in the models by Thornley *et al.* (1995), Schwinning & Parsons (1996a), as well as in the model presented in Chapter 2. However, this result is less surprising when it is taken into consideration that the impacts of *inter alia* other nutrients, of the

water status, the soil type or the soil pH, had not been incorporated in either of these models. In other words, the predicted dependence of ecosystem stability on nitrogen dynamics in fact originated from the very same assumption by the modellers. Far from implying that these predictions would consequently be without value, this relationship between the initial assumptions and the predictions of simulation models merely stresses the need to incorporate more of the major ecosystem properties, as identified in long-term experiments. To date, most simulation models have focussed mainly on the ecosystem properties above ground-level. The analysis of the stability of the ecosystems in the PGE suggests that soil processes, and especially pH dependent soil processes, may require more attention in grassland simulation models.

*8.3.2 Long-term experiments (> 40 years)*

Indeed the use of long-term experiments has proved indispensable for the identification of stabilising and destabilising management factors, and hence for the prototyping of structural management strategies. It has been explained extensively (Chapters 2, 3) that the yield fluctuations observed during short-term experiments (< 5 years) are rather a reflection of the stability of the environment than of the stability of the ecosystems observed. Only for ecosystems in long-term experiments (> 40 years), the effects of the environmental variability could be segregated from the extrinsic stability levels. Consequently, the mathematical framework presented in this thesis exclusively enabled the direct analysis of the causes of the stability or instability of each ecosystem. Considering the large number of ecosystems in the PGE and the Ossekampen which have not been studied in this thesis, as well as the existence of other long-term experiments across Europe, the direct insight into ecosystem stability may indeed be increased rapidly by applying the framework to these other ecosystems. Ultimately, it is conceivable that the framework is equally applicable to the analysis of the stability of ecosystems, other than grassland ecosystems.

*8.3.3 Short-term experiments (< 5 years)*

In spite of the limitations exemplified above, the role of short-term experiments in analysing grassland stability should not be underestimated. At the very least, the numerous studies quoted in this study have provided a solid basis for the prototyping of dynamic management strategies, with which the performance of white clover can be controlled on the short term. Moreover, the importance of these studies in the analysis of the productivity, as opposed to the stability, of mixed grasslands does not need further clarification. Perhaps most importantly, the results of short-term experiments do not only enable the validation, but also the construction of grassland simulation models. Therefore, these experiments and simulation models are mutually dependent: whereas experimental results are used to formulate the equations in simulation models, these models can put the same results into the context of the entire ecosystem and its environment.

Similar to these simulation models, however, the experimental study of grassland at field level only, is associated with a loss of large quantities of information. For instance, the effects of niche-differentiation, selective grazing, and plant escape mechanisms can only be detected at patch scale. In Chapters 6 and 7, methodologies were developed to analyse data generated by the Dry Weight Rank (DWR) method, in which large numbers of patches are individually observed. These methodologies enabled the segregation of the effects of e.g. urine depositions, and selective grazing, on the spatial heterogeneity of the herbage mass of each grassland species (Chapter 6), as well as the segregation of the niche-differentiation and the direct competition between perennial ryegrass, white clover, and creeping bentgrass (Chapter 7). Therefore, the use of the DWR method disclosed a wealth of information on the behaviour of mixed grasslands, by the rapid recording of the botanical composition and of the herbage masses of individual patches. However, the analysis of the DWR data was complicated by the fact that the locations of the quadrats used for the observations were chosen randomly during each observation period. More straight-forward and precise results may be expected, when quadrats are consistently placed at fixed locations, instead.

In conclusion, as envisaged in the General introduction (Chapter 1), this thesis has developed a new concept of the production stability of mixed grasslands, as well as methodologies with which this stability can be analysed, using simulation models, short-term experiments, or long-term experiments. It has foremost provided a "language" for the analysis of grassland stability and should therefore be considered as a precursor for further research. Considering the large number of grassland experiments reported in the literature, as well as the rapidly increasing computer power, it is envisaged that these methodologies can aid to provide a profound insight into the stability of mixed grasslands. Ultimately, it is hoped that this insight will lead to the development of additional management strategies, which improve the reliability of mixed grasslands, and hence their appeal to the farming community.

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# Summary

Recent years have seen a renewed interest in the use of white clover (*Trifolium repens*) in grasslands as a more sustainable alternative to fertiliser nitrogen inputs. However, these mixed grasslands have frequently been associated with fluctuating yields, and hence with an unreliable herbage production. New management strategies are required to sustain the production stability of mixed grasslands. Whereas the productivity of grass monocultures relies on abiotic nutrient inputs, mixed swards largely depend on the biotic processes involved in the fixation and mineralisation of nitrogen. Therefore the prototyping of management strategies for mixed grassland requires an understanding and analysis of the entire grassland ecosystem, of the temporal and spatial interactions between its internal processes, and of its interactions with the environment.

The stability of mixed grasslands over time was studied in Part I. In Chapter 2, the internal ecosystem processes and properties regulating stability were reviewed and analysed using a simple simulation model. Niche-differentiation, the dependence of grass species on white clover for their nitrogen supply, and plant mechanisms which allow a partial "escape" from grazing, were found to stabilise the herbage production of mixed swards. Conversely, competition for light, the delay between the fixation of nitrogen by white clover and its availability to other species, and the selective grazing of white clover were identified as destabilising factors.

Individual grassland patches which show an oscillating herbage production, may compensate for each other when these oscillations are set "out of phase" by frequent and local disturbances, such as manure and urine depositions. This compensation may lead to a stable herbage production at field scale, depending on the management regime.

The stability of mixed grassland changed drastically when the impact of environmental fluctuations on the ecosystem was considered. A discrimination was made between structured, i.e. seasonal, environmental fluctuations and stochastic fluctuations. Intrinsically stable ecosystems remain stable in the face of structured environmental fluctuations, but are destabilised by stochastic fluctuations. In contrast, intrinsically unstable systems are stabilised by structured fluctuations, but may be either further destabilised or stabilised by stochastic fluctuations, depending on the timing of individual environmental events.

Considering the large impact of coincidental environmental events on the stability of yields, a new concept of grassland stability was proposed. The *intrinsic stability* was defined as the stability of ecosystems in a hypothetical constant environment, and hence depends merely on internal system properties. The *extrinsic* stability was defined as the stability of ecosystems subjected to seasonal,

but not to stochastic fluctuations. The stability of systems in the face of both seasonal and stochastic fluctuations, as measured in experiments, was referred to as the *actual* stability. It was explained that the level of this actual stability may change over time, and is a reflection of the variability of the environment, rather than of the ecosystem or of its management. The extrinsic stability level is a more reliable indicator of system stability instead, allowing for the analysis of the effects of management strategies on the stability of production.

In Chapter 3, a mathematical framework was presented with which the extrinsic and intrinsic stability levels can be deducted from yield patterns observed in long-term experiments. This deduction allows for the segregation of the effects of internal ecosystem processes and of environmental fluctuations on the stability of yields. Consequently, the impact of management strategies can be analysed from a comparison of the extrinsic stability of ecosystems under different management regimes.

In Chapter 4, this framework was applied to the yield data of a number of plots in two long-term (>40 years) experiments, i.e. the Park Grass Experiment (UK) and the Ossekampen (The Netherlands). Regular lime applications and a grazing regime were identified as management strategies increasing the extrinsic stability. In both experiments, only small and inconsistent effects of fertiliser treatments on the stability were detected. The ecosystem which received farm yard manure showed a less stable production than the ecosystem receiving equal amounts of mineral nitrogen. It was consequently argued that the availability and turnover rates of nutrients largely define the stability of mixed grasslands.

In Part II, spatial interactions between plant species and between plants and the grazing animals were explored. Chapter 5 studied vertical interactions between perennial ryegrass (*Lolium perenne*) and white clover by the construction of a mechanistic simulation model, with which the vertical distributions of the lamina material and of the total leaf material of both species can be successfully simulated for a wide range of swards, subjected to a variety of management regimes. This model uses simple morphological plant characteristics as input variables, and can readily be incorporated into existing grassland simulation models, in order to increase their accuracy and flexibility in the simulation of competition for light and grazing.

The lateral heterogeneity of mixed swards, as well as its dependence on the management regime, was quantified and analysed in Chapter 6, using data generated by the Dry Weight Rank method for botanical assessment of mixed pastures. The heterogeneity of the total herbage mass was highest after cutting and topping of swards, and after lenient grazing by sheep, and lowest under

strip-grazing by these animals. Conversely, the heterogeneity of the white clover herbage mass was maximal under strip-grazing, and was lower under the other management regimes. It was argued that the stability of mixed grasslands depends primarily on this heterogeneity of white clover, and can hence be increased under strip-grazing.

Spatial interactions between grassland species were further explored in Chapter 7, again using data produced by the Dry Weight Rank method. A data analysis methodology was presented, which discriminates the extents of niche-differentiation and direct competition between perennial ryegrass, white clover, and creeping bentgrass (*Agrostis stolonifera*). Under a wide range of management regimes, white clover was excluded actively by creeping bentgrass by direct competition, whereas it showed a high compatibility with perennial ryegrass. The niches of these three species largely overlapped with respect to the grassland management regime. Niche-differentiation between white clover and creeping bentgrass in response to management was only observed between two management extremities. Whereas the performance of white clover was increased under a cutting regime, creeping bentgrass prevailed under lenient grazing. As a result, a sequence of silage cuts may be the only management tool to prevent creeping bentgrass infestations in grasslands.

It was finally argued that two types of management strategies are required in order to achieve production stability in mixed grasslands. Structural management strategies can be prototyped and are aimed to increase the extrinsic stability of grassland ecosystems. These strategies include regular lime applications, maximisation of the grazed area, and the use of mixtures of grassland species and varieties which show niche-differentiation in respect to seasonal growth, rooting patterns, or in response to stress factors or to management. Dynamic management strategies are required to counteract instabilities caused by either abiotic or biotic environmental events, such as extreme weather conditions or weed infestations. Due to the individuality of each farm ecosystem and its environment, these dynamic management strategies cannot be generalised, but instead require a familiarity of farmers with their ecosystems.

# Samenvatting

Gedurende de laatste jaren is de interesse toegenomen in het gebruik van witte klaver (*Trifolium repens*) in graslanden, als een duurzaam alternatief voor het gebruik van kunstmeststikstof. Van gemengde grasbestanden wordt echter beweerd dat ze sterke opbrengstfluctuaties vertonen, en dat er dientengevolge sprake is van een onbetrouwbare productie. Nieuwe strategieën voor graslandbeheer zijn derhalve noodzakelijk voor handhaving van de productiestabiliteit van gemengde grasbestanden. De productiviteit van gemengde zodes hangt voornamelijk af van de biotische processen die een rol spelen in de fixatie en de mineralisatie van stikstof, in tegenstelling tot de productiviteit van grasmonocultures, die afhangt van (abiotische) nutriëntengiften. Voor de protypering van beheerstrategieën voor gemengde grasbestanden is het nodig om te beschikken over voldoende analytisch inzicht in het gehele graslandecosysteem, alsmede in de temporele en ruimtelijke interacties tussen de interne processen, en in de interacties met milieufactoren.

De stabiliteit van gemengde grasbestanden in de tijd werd bestudeerd in Deel I. In Hoofdstuk 2 werden de interne processen en eigenschappen van ecosystemen besproken en geanalyseerd aan de hand van een eenvoudig simulatiemodel. De productie van gemengde zodes bleek gestabiliseerd te worden door niche-differentiatie, door de afhankelijkheid van grassoorten van witte klaver voor hun stikstofvoorziening, en door mechanismen waarmee plantensoorten gedeeltelijk kunnen "ontsnappen" aan begrazing. Lichtconcurrentie, het tijdsinterval tussen de stikstoffixatie door witte klaver en de beschikbaarheid van deze stikstof voor andere plantensoorten, en de selectieve begrazing van witte klaver werden daarentegen als destabiliserende factoren geïdentificeerd.

Indien de productie van plekken in het grasland oscilleert, dan kunnen deze plekken elkaar compenseren als ze "uit fase" worden gebracht door frequente, lokale verstoringen, zoals de depositie van mest en urine. Afhankelijk van het graslandbeheer kan deze compensatie tot een stabiele productie van het gehele veld leiden.

De stabiliteit van gemengde grasbestanden veranderde drastisch wanneer het effect van milieufluctuaties op het ecosysteem in acht werd genomen. Er werd onderscheid gemaakt tussen gestructureerde fluctuaties, d.w.z. seizoensfluctuaties, en stochastische fluctuaties. Intrinsiek stabiele ecosystemen blijven stabiel onder gestructureerde milieufluctuaties, maar worden gedestabiliseerd door stochastische fluctuaties. Intrinsiek instabiele systemen worden daarentegen gedestabiliseerd door gestructureerde fluctuaties, maar kunnen hetzij verder worden gedestabiliseerd, hetzij worden gestabiliseerd door stochastische fluctuaties, afhankelijk van het tijdstip waarop deze optreden.

Vanwege het grote effect van willekeurige milieuomstandigheden op de productiestabiliteit,

werd een nieuw concept voorgesteld voor graslandstabiliteit. De *intrinsieke* stabiliteit werd gedefinieerd als de stabiliteit van ecosystemen in een hypothetisch, constant milieu. Deze stabiliteit hangt dientengevolge alleen af van interne systeemeigenschappen. De *extrinsieke* stabiliteit werd gedefineerd als de stabiliteit van ecosystemen onder enkel gestructureerde fluctuaties. De stabiliteit van ecosystemen die onderworpen zijn aan zowel gestructureerde als stochastische fluctuaties, d.w.z. de stabiliteit zoals die gemeten wordt in experimenten, werd de *actuele* stabiliteit genoemd. Het niveau van deze actuele stabiliteit kan veranderen in de tijd, en is meer een reflectie van de variabiliteit van het milieu, dan van het ecosysteem of van het beheer. Daarentegen is het extrinsieke stabiliteitsniveau een betrouwbaarder indicator van systeemstabiliteit, hetgeen een analyse mogelijk maakt van het effect van beheerstrategieën op de productiestabiliteit.

In Hoofdstuk 3 werd een mathematisch raamwerk gepresenteerd, waarmee de extrinsieke en de intrinsieke stabiliteitsniveaus kunnen worden afgeleid van de opbrengstpatronen die werden waargenomen in langjarige experimenten. Deze afleiding maakt het mogelijk om de effecten van de interne ecosysteemprocessen op de productiestabiliteit te onderscheiden van de effecten van milieufluctuaties. Het effect van beheerstrategieën kan vervolgens worden geanalyseerd door de extrinsieke stabiliteit van ecosystemen onder verschillende beheersystemen te vergelijken.

In Hoofdstuk 4 werd dit raamwerk toegepast op de opbrengstgegevens van een aantal proefvlakken in twee langjarige experimenten (> 40 jaar), te weten het Park Grass Experiment in het Verenigd Koninkrijk en de Ossekampen in Nederland. Regelmatige bekalking en begrazing bleken beheerstrategieën te zijn die de extrinsieke stabiliteit verhogen. In beide experimenten werden slechts kleine, inconsistente effecten van kunstmestbehandelingen op de stabiliteit waargenomen. De productie van het ecosysteem waaraan stalmest werd toegediend was minder stabiel dan de productie van het ecosysteem dat een gelijke hoeveelheid aan minerale stikstof ontving. Kennelijk wordt de stabiliteit van gemengde grasbestanden voornamelijk gereguleerd door de beschikbaarheid en de omzettingssnelheid van nutriënten.

In Deel II werden de ruimtelijke interacties tussen plantensoorten, en tussen planten en begrazers onderzocht. In Hoofdstuk 5 werden de verticale interacties tussen Engels raaigras (*Lolium perenne*) en witte klaver bestudeerd, aan de hand van de constructie van een mechanistisch simulatiemodel. Met dit model kan de verticale distributie van de bladschijven en van de gehele bladeren van beide soorten met succes worden gesimuleerd voor een breed scala aan grasbestanden, onder een groot aantal types beheer. Dit model gebruikt eenvoudige morfologische planteigenschappen als inputvariabelen, en kan direct in bestaande graslandsimulatiemodellen worden opgenomen om de nauwkeurigheid en flexibiliteit te verbeteren van de simulatie van

lichtconcurrentie en begrazing.

De laterale heterogeniteit van gemengde zodes, alsmede de relatie van deze heterogeniteit tot het graslandbeheer, werd gekwantificeerd en geanalyseerd in Hoofdstuk 6, met behulp van gegevens die gegenereerd waren met de Dry Weight Rank methode voor het vaststellen van de botanische samenstelling van gemengde graslanden. De heterogeniteit van het gewas als geheel bleek het hoogst na een snede of na bloten, en onder lichte begrazing door schapen, en het laagst onder stripbegrazing. De heterogeniteit van de witte klavermassa was daarentegen maximaal onder stripbegrazing, en lager onder de overige beheersystemen. De stabiliteit van gemengde grasbestanden hangt voornamelijk af van deze heterogeniteit van witte klaver, en deze kan dus verhoogd worden door stripbegrazing.

De ruimtelijke interacties tussen graslandsoorten werden verder onderzocht in Hoofdstuk 7, wederom met gebruik van gegevens die verzameld waren met de Dry Weight Rank methode. Een methodologie werd gepresenteerd voor de analyse van gegevens, waarmee een onderscheid gemaakt kan worden tussen de mate van niche-differentiatie en directe concurrentie tussen Engels raaigras, witte klaver en wit struisgras (*Agrostis stolonifera*). Onder een breed scala aan beheersystemen werd witte klaver actief onderdrukt in directe concurrentie met wit struisgras, terwijl het zeer compatibel was met Engels raaigras. De beheersniches van deze drie soorten bleken elkaar grotendeels te overlappen. Slechts tussen twee extreme vormen van beheer werd niche-differentiatie met betrekking tot het beheer waargenomen tussen witte klaver en wit struisgras. De groei van witte klaver werd versterkt onder een maairegime, terwijl dat van wit struisgras werd gestimuleerd onder lichte begrazing. Mogelijk kunnen invasies van wit struisgras in graslanden daarom alleen worden voorkomen door een reeks maaisnedes.

Productiestabiliteit in graslanden vraagt om twee typen beheerstrategieën. Structurele beheerstrategieën die er op gericht zijn om de extrinsieke stabiliteit van graslandecosystemen te verhogen kunnen worden geprototypeerd. Voorbeelden van deze strategieën zijn regelmatige bekalking, een beheer zoveel mogelijk gericht op begrazing, en het gebruik van mengsels van graslandplanten en cultivars die niche-differentiatie vertonen met betrekking tot seizoensgebonden groei, bewortelingspatronen, stressfactoren of het graslandbeheer. Dynamische beheerstrategieën zijn nodig om instabiliteiten tegen te gaan die worden veroorzaakt door abiotische en biotische milieuomstandigheden, zoals extreme weersomstandigheden en onkruidinvasies. Gezien de uniciteit van ieder agrarisch ecosysteem en zijn milieu is het niet mogelijk om deze dynamische beheerstrategieën te generaliseren. In plaats daarvan verlangen deze een bekendheid van agrariërs met hun ecosysteem.

# Curriculum Vitae

Rogier Patrick Olaf Schulte was born on 20th May 1974 in Twello, The Netherlands. He graduated from the athenaeum of the Geert Groote College in Deventer, in 1992, and consequently studied Biology at the Wageningen Agricultural University. Graduated in 1995, he specialised on the analysis of low-input grassland ecosystems, and achieved his MSc in Biology in September 1997. In November 1997, he was employed by Teagasc as a Walsh-Fellow at the Johnstown Castle Environmental Research Centre in Wexford, Ireland, where he carried out a PhD for the Department of Plant Sciences of Wageningen University in Wageningen, The Netherlands. He is currently employed by Teagasc as a research officer at the same centre.